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PAUL A. FRYXELL 135

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THE BOTANICAL REVIEW

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MODE OF REPRODUCTION OF HIGHER PLANTS

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I. INTRODUCTION

Floral biology has received the attention of many investigators. Prominent among the early students were Sprengel (402), Müller (300) and Knuth (242). The monumental three-volume work by the last mentioned ably summarizes the knowledge of the nineteenth century and before; it is an immense reservoir of information on the subject. The viewpoint of these workers and of their contemporaries, as well as of some more recent workers (e.g., Jones (219), Gibbs (141), Hagerup (156)), is that of floral mechanism and structural adaptation rather than of pollination dynamics approached experimentally. Their viewpoint is fundamentally morphological instead of functional and only imperfectly represents the latter. Also one finds a thread of thought that plants ought to be cross-pollinated, stemming perhaps from the observations of Darwin (92), which lends some bias to their observations.

More recently, however, the functional viewpoint has been recognized as having greater value in understanding the pollination dynamics of populations. Plant breeders have found it necessary to measure rates of natural crossing in order to understand the breeding systems of the species with which they work; seed producers have been interested in the question of the necessity for and the degree of crop isolation; systematists have learned that reproductive behavior is a valuable key in unlocking evolutionary history and explaining evolutionary mechanisms. Consequently, the viewpoint has changed, and much work has been done from a new orientation. It is the purpose of this paper to review this work, paying particular attention to the methodology of studying population breeding structure and to summarize existing knowledge of the breeding structure of species of phanerogams.

Within the past half-century a great deal of work has been done in measuring the rates of natural cross-pollination of various species—generally species of economic interest. This material forms a major portion of the present review. In some cases the methodological techniques employed have been relatively crude; in others they have been more refined. (See pp. 143 ff.) Self-incompatibility has been the subject of intensive investigations (see reviews by Lewis (260), East 104), Bateman (30), Sears (385)), and is a subject which has a direct bearing on population breeding structure. In addition, the phenomenon of apomixis has received increasing attention since the beginning of the present century (see reviews by Stebbins (404), Gustafsson (150), Nygren (314)). Apomixis, being the absence of sexuality, is a subject of considerable importance in evaluating breeding systems. The exhaustive monograph by Gustafsson (150) is an invaluable source of references to the botanist interested in reproductive biology. The work done in these several fields has been quite extensive; it is intended that the present review bring the results of much of it together, from the viewpoint just described, and make these results more readily available to interested students.

The older "morphological" viewpoint is, of course, related to the newer "functional" approach. Thus, for example, with a species which shows a structural adaptation for entomophily (e.g., *Medicago sativa*), we also find cross-pollination to be the rule from experimental studies. It is where no such agreement is to be

found, however, that the functional viewpoint is preferable. Nothing in the floral anatomy of *Cichorium intybus*, for example, indicates that self-incompatibility is the rule in this species, nor can one differentiate the floral behavior of this principally cross-pollinated species from that of the partially cross-pollinated, partially self-pollinated *C. endivia*, except by experimental studies. Further, a consideration of floral adaptions does not give any indications of the possible existence of apomixis, except in certain obvious cases of vegetative apomixis, as in *Allium sativum*.

Finally, species which have evolved a marked adaptation for cross-pollination may have subsequently discarded the function while retaining the structure. Such a history seems to have occurred in *Orchis maculata* (276), for example. In *Marcgravia* (14) it seems that botanists had been in error in deducing function from structure, either through ascribing the wrong function (in this case the attraction of insects and birds to accomplish cross-pollination) to the structure or through ascribing a discarded function to it.

Consequently we may conclude that, while structural considerations frequently may be indicative of functional behavior, the only case where one may obtain assurance is in dioecious species which must be cross-pollinated, and even then one must retain a reservation in favor of the possibility of apomixis (as, for example, in *Simmondsia chinensis* (139)). In view of these considerations and of the fact that the preponderance of phanerogams are perfect-flowered (or hermaphroditic), as shown by Yampolsky and Yampolsky (476), the viewpoint of pollination dynamics appears preferable to the consideration of structure and adaption in evaluating the mode of reproduction among higher plants.

II. IMPORTANCE OF KNOWLEDGE OF REPRODUCTIVE MODE

The plant breeder is particularly concerned with the mode of reproduction of a given plant species. It must be recognized, however, that this is a two-fold problem. He is interested first in the production of new and improved forms; and secondly in the maintenance of this new material in stabilized conditions over a period of time in commercial plantings. As a result he must take cognizance of two aspects of reproduction: (*a*) the natural mode of pollination of the species, (*b*) the usual (or possible) methods

of propagation. The latter point is principally concerned with the question of whether propagation is by sexual or asexual means; the former presents a number of possible alternatives.

A knowledge of these two points is of importance to the breeder in that it largely determines both his procedures and objectives in pursuing a breeding program with a given species. The natural mode of pollination delimits the type of mating system which occurs naturally in field populations as well as the types of mating systems which the breeder can impose on these populations. Consequently the methods of breeding which he uses in producing new and improved material depend upon the natural mode of pollination of the species. On the other hand, his objectives (in terms of the maintenance of new and improved material) depend largely on the mode of propagation of the crop. However, the methods of breeding also depend upon a knowledge of the mode of propagation, for breeding procedures must take notice of breeding objectives. For example, both alfalfa and apples (*Medicago sativa* and *Malus sylvestris*) are normally cross-pollinated crops, but the procedures used by alfalfa breeders differ widely from those of apple breeders. This difference arises largely from a difference in objectives: alfalfa is sexually propagated and the objective is an interbreeding population, while apples are asexually propagated and the objective is a single superior individual. Thus a knowledge of the mode of propagation is of great importance to the breeder; however, the natural mode of pollination will be the principal concern of the following discussion.

A knowledge of natural mode of pollination is also of importance to systematists, plant geographers, ecologists, horticulturists and students in other branches of botanical inquiry. Examples of related problems include the applied horticultural problem of fruit-set as a function of self-incomptability (148), the dynamics of interbreeding populations, the maintenance or loss of variability of wild populations, particularly in the face of changing ecological conditions (18), etc.

By way of sketching some of the more important of these considerations, let us first note the widespread distribution of sexuality in the biological world. Sexuality obviously has a strong selective advantage, and this advantage is interpretable in terms of providing genetic recombinations and thus variation in popu-

lations which are sexual. This genetic variation allows for evolutionary plasticity in the face of changing environmental conditions and is, hence, of selective advantage. It is apparent that only outbreeders benefit from this phenomenon; inbreeders and apomicts do not. The latter two types have developed mechanisms which enable them to reproduce more certainly, an advantage under certain conditions, but in developing this advantage they have sacrificed the advantage of variation.* Thus we see that the breeding mechanism which a species exhibits exerts an influence on its evolutionary potentialities (in terms of adaptability to new or changing environments), and conversely that the environment exhibits an influence on the breeding mechanism which will be most advantageous to a given species. These relationships are discussed more fully by Baker (18, 21) and Heslop-Harrison (183a).

One might develop these relationships even further by noting that even in outbreeding species, various types of population breeding structure may obtain. The limits of free gene exchange might be over relatively large or relatively restricted portions of the population. These various conditions would in turn have various consequences in terms of evolutionary development. This problem is outlined more fully by Fryxell (127).

By way of illustration, one might cite the comparison made by Stevens (407) of estimates of disease loss of various crop plants, classified by mode of reproduction. He showed that there was heavier disease loss for vegetatively propagated crops than for seed propagated crops. Among the seed propagated crops, the self-pollinated species suffered heavier losses than outcrossed species. The same relationship was observed when comparing the number of virus diseases observed on various crop species. It is not difficult to extrapolate the conclusions reached from these cultivated crop plants to naturally occurring populations.

III. MEASUREMENT OF NATURAL CROSSING

Measurement of the natural mode of pollination of plants is in part a matter of refined experimental procedure and in part a matter of crude classification. That is, some plants must be tested experimentally where no simple criterion is available, while others

* *Lespedeza* spp. seem to have retained both advantages (see p. 153). The same is also true for numerous facultative apomicts.

may be categorized very easily on the basis of some easily evaluated trait. These "categories of elimination" are:

DIOECIOUS PLANTS. It is quite apparent that such species would be entirely cross-pollinated. Further, their sexual dimorphism poses certain unique problems to the plant breeder. The principal caution in classifying a species in this category is that some species are incompletely dioecious or polygamous and occasionally or regularly produce monoecious or hermaphroditic individuals. In some species which show a direct and simple genetic control of such sexual polymorphism (e.g., *Luffa acutangula* and *Origanum vulgare*) and where this polymorphism is relatively stable, one can, of course, deduce that cross-pollination must be the rule on the basis of the genotypes involved. There is also the possibility that apomixis exists, as already pointed out for *Simmondsia chinensis*, as an example.

APOMICTIC PLANTS. To demonstrate that a given species is apomictic is not always simple, depending in part on the type of apomixis concerned. However, where such demonstrations have been made, classification is simple in that pollination is not operable, except possibly in a stimulatory capacity. Difficulties arise here, in both classification and breeding, for those species where apomixis and sexuality occur in an inseparable mixture, as in *Poa pratensis*. It is important to distinguish such facultative apomicts from obligate apomicts (see Lawrence (252), p. 184), the latter having no known sexual phase, e.g., *Allium sativum*. The picture is further complicated where some ecotypes of a species are apomictic, either facultative or obligate, while other ecotypes are fully sexual, e.g., *Bouteloua curtipendula*.

SELF-INCOMPATIBLE PLANTS. Species in which self-incompatibility occurs will be entirely cross-pollinated. Unfortunately for the classifier, degrees of self-incompatibility exist (104, 396, 416) from weak to strong; and in other species, where self-sterility is a strong barrier, individuals of complete self-fertility are known, e.g.,

DICHOGAMOUS PLANTS. Both protogyny and protandry yield the same result—cross-pollination. One must be careful to determine whether the dichogamy described (or observed) for a species refers to the individual flower or to the individual organism *Trifolium pratense*.

(414), as it must for consideration in terms of self- and cross-pollination. Care must also be taken to determine whether such dichogamy is complete or partial, i.e., overlapping. (Cf. synchronous and reciprocating dichogamy (416).)

CLEISTOGAMOUS PLANTS. Plants of this group are completely self-pollinated. However, considerable caution must be exercised in arguing mode of pollination from floral morphology, as already pointed out in the Introduction. Pollinating agents can be very unobtrusive, e.g., thrips (6, 153), and a consideration of such agencies together with the widespread phenomenon of self-sterility requires cautious interpretation and preferably experimental evidence.

Elimination of these five categories still leaves those species which are chasmogamous and self-fertile, and are neither dichogamous, dioecious nor apomictic. Such species could fall anywhere on the range from entirely self-pollinated to entirely cross-pollinated. To determine where on this range they fall requires experimental evidence; the measurement made is usually that of "per cent natural crossing". It will be convenient to divide this range arbitrarily into three parts for those plants which are (*a*) principally cross-pollinated, (*b*) partially self-, partially cross-pollinated, and (*c*) principally self-pollinated.

1. Use of Genetic Markers

For the measurement of per cent natural crossing, it is desirable to have a tool in the form of a genetic marker or markers of known inheritance, although a detectable hybrid is all that is essential. Without such markers it is more difficult to gather and interpret experimental data with assurance. Marker genes that are fully appropriate are sometimes difficult to obtain, for there are several attributes which it is desirable that they possess.

It is desirable for a marker gene to have a phenotypic effect that is easily classifiable in the seedling stage. With such a marker the experimenter can handle relatively large amounts of material more easily and therefore can estimate the per cent natural crossing more precisely.

It is desirable that the marker gene be recessive to the allele generally found in field plantings or natural populations of the species. This experimental structure eliminates the necessity for

isolation of the experimental material. Such isolation is both an added requirement for the experimenter to meet and a situation which is possibly atypical of natural pollination conditions (406).

Finally, the strain used as a marker strain should have no effects, of itself, on the amount of natural cross-pollination. This relationship is difficult to assess without detailed study. Genetic differences are known to exist with respect to natural crossing (see pp. 153 ff.). Such differences, where they exist, may be assigned to the marker gene itself, either through its own pleiotropic effects or through the effects of other genes closely linked to it, or to the chance association of other genes with the marker gene in the marker strain used. Though not a rigorous solution, an estimate can be made of the effects of the marker stock in terms of any phenotypic differences which would clearly exert an influence on pollination, such as floral morphology, time of anthesis and number of flowers. More rigorous solutions will be discussed below.

Plants having a male-sterile genotype are sometimes used as test plants in measuring rates of natural cross-fertilization. This procedure may be satisfactory under certain circumstances but ought not be recommended generally. To conclude that a species exhibits a rate of natural crossing of X% because a male-sterile form of that species sets X% of a full complement of seed, is not fully defensible. A male-sterile plant, which produces no pollen, does not undergo the same pollination phenomena that a normal plant of the species does. Specifically, no account is taken of the effect of competition between self and foreign pollen in achieving fertilization. This competition may be in the form of different rates of germination or growth for self versus foreign pollen, or it may be in the different times at which self and foreign pollen are deposited on the stigma and begin germination, or it may be the result of different quantities of pollen being produced by different flowers. The latter has been shown by Stephens (405a) to be of importance. Thus an estimate of natural crossing made with the use of male-sterile testers may reflect information concerning self- and cross-pollination, but may be quite in error concerning self- and cross-fertilization (see p. 154), whereas a measurement made with a more "conventional" marker gene will tend to avoid this difficulty. In some cases these two types of measurements

may provide comparable results (cf. Jones' (216) and Kakizaki's (230) results with those of Rick (361) for *Lycopersicon esculentum*, for example), in which event the male-sterile approach has the distinct advantage of not requiring a progeny test. However, the two approaches may provide quite different results also, and this could be determined only by direct comparison.

2. Definition of Natural Crossing

In formulating experimental procedures for the measurement of natural crossing, it is necessary to state specifically what is meant by natural crossing. King and Brooks (236) present a discussion of the several viewpoints encountered in the discussion of pollination problems. Since the present discussion is oriented from a genetic viewpoint, it is clear that the basis of cross-pollination is the individual organism, not flowers within organisms, specific genotypes or any other unit.

It is pertinent at this point to distinguish between natural crossing, per se, here considered as intra-population crossing, and intervarietal crossing, which is inter-population crossing. One might define natural crossing as that which occurs between individuals within a population. The two phenomena (intra- and inter-population crossing) are related, but the distinction is not always made clear. Our present concern is with the former of these, though the latter is also of interest, particularly with relation to the problem of isolation for commercial seed increase of crop plants. In this connection see Bateman (26), Currence and Jenkins (86), Jones and Newell (218), Nicolaisen (310).

There are instances in the literature—all too frequently—which employ the phrase " natural crossing " to refer exclusively to interspecific crossing. This usage is in direct conflict with the more common usage described above and consequently is rejected as confusing. The question of priority of usage has not been examined, but in this light the use of " natural crossing " to mean " naturally occurring interspecific hybridization " is to be deplored.

3. Experimental Procedures

Probably the simplest and most satisfactory experimental procedure for the measurement of natural crossing is the use of a suitable monogenic recessive marker as a minority planting, inter-

spersed within a test field (50). Single plants are spaced at a sufficient distance so that cross-pollinations between two recessive plants are quite unlikely. Such pollinations would be cross-pollinations but would be indistinguishable from self-pollinations, and consequently the estimate of natural crossing obtained would be an under-estimate. With sufficiently wide spacing between the recessive individuals, it is apparent that all cross-fertilizations involving a recessive individual as maternal parent will result in phenotypically dominant offspring, while all self-fertilizations will produce recessives. Therefore, open-pollinated seed is harvested from the recessive individuals; it is grown and classified; and the per cent natural crossing is measured as the proportion of phenotypically dominant offspring. In this way the experimenter will have as many independent estimates of natural crossing as he has individual recessive plants in the field.

A common practice in measuring "natural crossing" is to assess the crossing which occurs between adjacent rows of a crop. This practice is followed because it is, in many ways, an experimentally simpler situation. However, it must be pointed out that this provides only a minimum estimate of natural crossing, for all within-row crosses which occur are cross-fertilizations but are not detected as such. Thus an under-estimate is obtained.

A modification of the first procedure has been used by the author (unpublished) in assessing natural crossing in cotton (*Gossypium hirsutum*) in New Mexico. The marker gene employed in this study is a recessive lethal. Since the homozygous recessives cannot be obtained, although they do survive the seedling stage and therefore can be classified, it is necessary to plant the heterozygote as the minority planting in a field test. Since the lethal allele is completely recessive, it is impossible to distinguish the heterozygotes from the homozygous dominants in an F_2 population, except from their progeny, and the test plants set out are therefore a mixture of AA and Aa in the proportion of one to two. The former are useless for the study and are discarded as soon as they are identified by progeny test. The latter provide an estimate of natural crossing and have the advantage of being at present phenotypically indistinguishable from the remainder of the field. They are considered, thus, as having little effect on natural crossing in themselves through such things as insect color preference,

for example. In practice the open-pollinated seed is harvested from the heterozygotes and grown and classified as before. The recessives are easily classified as chlorophyll-deficient and incapable of growing beyond the cotyledon stage. In the absence of cross-pollination the expected segregation is 3:1, normal to lethal; for complete cross-fertilization (no selfing) the seedlings would be all normal. The per cent natural crossing is estimated as

$$\frac{A-3a}{A+a}$$

where A is the number of normal seedlings and a the number of lethals.

This procedure was also used by Philp and Sherry (334) and Moffett (293a) in assessing the degree of natural crossing in *Acacia decurrens*. A naturally occurring recessive lethal, which is capable of germination and therefore of classification, was used by these workers. Since the marker gene was found in naturally occurring populations, it was not possible to space the test plants (heterozygotes) as a minority planting. Therefore the observed rate of natural crossing is a minimum estimate, as pointed out by the authors.

Stephens and Finkner (406) offer a procedure for estimating natural crossing. The proportion of heterozygotes expected in successive generations of a partially outcrossed population can be determined with the formula

$$h = \tfrac{1}{2}[(1-k)h' + k]$$

where h is the proportion of heterozygotes in one generation, h′ that in the preceding generation, and k the proportion of outcrossing or per cent natural crossing. It follows that k can be estimated as

$$k = \frac{2h-h'}{1-h'}$$

when one has observational data on h and h′. A simple procedure for obtaining this is to grow an F_2 population (where the expected value of h′ is 0.50) and obtain its bulked, open-pollinated progeny. The proportion of heterozygotes in this population provides a value for h. In general, any population (except as noted below)

segregating for a suitable marker gene (grown in isolation) and its open-pollinated progeny would provide data for the estimation of k, the per cent natural crossing, by the use of this formula.

Ali and Hadley (5) present a formula for estimating the proportion of heterozygosity in populations with various proportions of self- and cross-fertilization. The formula is

$$H = 2pq\left[\frac{a(1-r^n)}{1-r}\right] + hr^n$$

where p and q (= 1 − p) are gene frequencies of alternative alleles, a = the proportion of outcrossing, $r = \frac{1-a}{2}$, h = the proportion of heterozygosity in the initial generation, H = the proportion of heterozygosity in the final generation, and n = the number of generations intervening between h and H. This, then, is seen to be a generalization of the formula presented by Stephens and Finkner (406). In comparing the two formulas, it becomes apparent that they are not identical and that Stephens and Finkner (406) have omitted an important assumption. The formula of Ali and Hadley (5) reduces to

$$H = \tfrac{1}{2}[4pqa + h(1-a)]$$

when n = 1, which is the special case considered by Stephens and Finkner (406). This formula, translated into the symbolism of the latter authors, becomes

$$h = \tfrac{1}{2}[4pqk + h'(1-k)]$$

while their original formula is

$$h = \tfrac{1}{2}[k + h'(1-k)].$$

Thus the original formula given by Stephens and Finkner is valid only where 4pq = 1, which is to say when $p = q = \frac{1}{2}$. Any departure from this value for p will produce a biased estimate of k, the proportion of outcrossing. Thus the formula they present is not so widely applicable as is suggested. The limits of applicability and the nature of the bias have been considered by Fryxell (129).

An estimate obtained from data of this sort will be free from bias arising from fortuitous association of the marker gene with

other genes which themselves affect the amount of natural crossing, because the data are obtained from a segregating population, and any such influence will be balanced out overall by recombination and will not be associated with the marker. However, as pointed out and elaborated by Stephens and Finkner (406), the method is insensitive in that outcrossing affects the progeny of only a portion of the original population, viz., the proportion with the recessive genotype. Further, any genetic effects which may exist of the marker itself on natural crossing, whether pleiotropic or due to close linkage, are not removed from such an estimate.* However, an elaboration of the method provides a means of estimating such effects. By the use of a population segregating for several marker genes, none of which is linked, as many independent estimates of natural crossing can be made with the method just described as there are segregating marker genes in the population. Clearly, if none of these markers has any effect on natural crossing from linkage or pleiotropy, none of the estimates will differ significantly. On the other hand, if significant differences are detected, it will generally be possible to determine which of the marker genes are influencing the estimate of natural crossing and in what manner they are producing a bias. In this way it should be possible to evaluate marker genes and select those not influencing natural crossing for further use.

A somewhat similar procedure is presented by Li (263) and amplified by Fyfe and Bailey (131), which uses a monofactorial dominant segregation. By scoring a sample of plants obtained from a naturally pollinated population and by growing and scoring progenies of these plants for the segregating gene in question, it is possible to estimate the rate of natural crossing in the following way. If the original sample of parent plants is found to occur in the proportions:

Genotype	Proportion
NN	a
Nn	b
nn	c
Total	n_1

* Bryan and Marriott (50) suggest the use of marker stocks reciprocally to obviate this difficulty.

then the following maximum likelihood estimates can be made:

$$\hat{p}_1 = \frac{(2a+b)}{2n_1}$$

$$\hat{f}_1 = \frac{(4ac-b^2)}{(2a+b)(b+2c)}$$

where p is the gametic frequency of allele N and where f is the coefficient of inbreeding (similar to Wright's F for a population in equilibrium) which is related to the rate of cross-fertilization, α, in the following way:

$$f = \frac{(1-\alpha)}{(1+\alpha)}$$

or

$$\alpha = \frac{(1-f)}{(1+f)}$$

The progenies of NN parents will give no information. If the progenies of Nn individuals are found to segregate in the proportion:

Phenotype	Proportion
N	e
n	d
Total	n_2

and the progenies of nn individuals segregate in the proportion:

Phenotype	Proportion
N	l
n	k
Total	n_3

then additional maximum likelihood estimates of the parameters are as follows:

$$\hat{p}_2 = \left[\frac{4dn_3}{ln_2} - \frac{n_3}{l+2}\right]^{-1}$$

$$\hat{f}_2 = \left[\frac{2d}{n_2} + \frac{l}{n_3}\right]^{-1} - 1$$

The subscripts 1 and 2, applied to the estimators $\hat{p}$ and $\hat{f}$, denote

estimates obtained from the parent plants and progenies, respectively. Thus two independent maximum likelihood estimates of the rate of natural crossing, a_1 and a_2, can be readily obtained. Fyfe and Bailey (131) also give formulas for the variance of these estimates and give an application to data obtained from *Vicia faba*. For a fuller treatment of this problem, including the derivation of formulas and an example of combined estimation, the reader is referred to the original.

Three advantages of this method of measuring natural crossing are listed as (*a*) the material from which the information is obtained need not be especially grown for the purpose; routine progeny testing as practiced in most plant breeding programs is sufficient; (*b*) the information obtained refers to fertilization occurring within the population itself; and (*c*) the maximum likelihood estimates obtained are consistent and efficient in the statistical sense.

As previously stated (p. 143), the unit of interest in natural crossing studies is the individual organism. A necessary modification of this viewpoint is offered by Hutchinson and Lawes (199). They present data taken from a study of natural crossing in *Gossypium hirsutum* in Africa showing that natural crossing, as measured on a per plant basis, may be quite misleading in certain instances. In the material studied the overall per cent natural crossing (on a per plant basis) was small, on the order of 11%. However, when the data were examined on a per fruit basis, a sharp discontinuity was encountered. The majority of fruits showed no outcrossing; a minority of fruits had a relatively large amount of outcrossing, of the order of 50%. The weighted average of these, of course, gave a per plant estimate of about 11%. This situation apparently resulted from the effective insect population being far less than adequate for coverage of the flower population. As a result, only a scattering of flowers were visited, but these exhibited a relatively high degree of natural crossing as a result of the visit. For a plant breeder working under similar conditions, where seed of selected plants might be obtained from single fruits, this would have important consequences, especially if there were a strong selection for heterozygotes, for example. It must be recognized, however, that such a situation would arise only in rather special instances, depending on such variables as

number of flowers per plant and flower size for the species considered, size of effective pollinator population relative to the flower population, as well as temporal considerations concerned with flowering sequence.

IV. FACTORS AFFECTING REPRODUCTIVE MODE

For a given group of plants, the reproductive method varies from place to place and from time to time. These spatial and temporal variations in breeding method are both environmentally and genetically conditioned. Some of them are discussed by Haskell (177). It will not be possible at this time to present a detailed consideration of the various agencies which influence the breeding system; only the most salient will be considered, by way of pointing out cautions to be observed in analyzing and interpreting given populations.

1. Entomological Influences

It is of course apparent that for entomophilous plants, variations in the number, kinds or activities of the insect pollen vectors may bring about variations in the breeding system of the plant population. Perhaps a more meaningful measurement of vector population size is relative to the size of the population of flowers which potentially may be visited, instead of simply as an absolute value. Stephens and Finkner (406) have defined "the effective bee population" as "the ratio of the number of bees to the number of cotton flowers in a given area", in the case of *Gossypium* where bees are considered the most important pollen vectors. As a ratio, then, this measurement is subject to fluctuations resulting from changes in the size of either the vector population or the flower population, and this might be expected to change cyclically through each growing season. A statistician may object to defining a population as a ratio, but biologically the definition is valid because the population concerned is an abstract one based on activity and is determined by the interaction of the two concrete populations of insects and flowers. This seems to be expressed most simply as a ratio.

Many species of entomophilous plants are visited by several species of insects, no one of which is of predominant importance as a pollen vector. Since different species of insects will gener-

ally differ in their patterns and rates of activity, a shift in relative proportions of the several insect species will result in a changed pollination pattern for the plant species. Similarly, changes in ecological conditions affecting a particular insect vector may result in changes in the activity pattern of this vector. Such things as changes in temperature, rainfall, food supply and activities of predators, may be reflected in changes in the pollination pattern of the plants which are visited.

Finkner (119) presents data indicating that pollen vector activity is random in isolated test plots of *Gossypium hirsutum*. This is interpreted as a lack of systematic pattern in the plant-to-plant visitation of the vector on a local level. It should not be interpreted as a randomness of visitation in the plant population as a whole, since, as appears obvious, an insect's activities are restricted to a finite area for any finite period of time. This is, indeed, brought out clearly by the observations of Stephens and Finkner (406) on the distribution of methylene blue by insect visitors. This dye was placed in a newly opened flower, and particles of it were distributed to neighboring flowers concurrent with pollen distribution by insect visitors. Subsequent observation of the distribution of the dye indicated that " as the distance from the dusted flower increased, both the proportion of the flowers carrying the dye and the amount of dye particles per flower decreased ". This indicates that the activities of the pollen vectors were geographically restricted, though, as Finkner's data (119) indicate, they were at random within this restriction. Drüsedau (100) also points out the geographical restriction of pollen vector activity in populations of *Coreopsis tinctoria*. This question of a spatial restriction on pollen distribution is considered further by Fryxell (127).

A non-uniform breeding structure was observed by Fryxell (128) in a partially cross-pollinated (entomophilous) population of *Gossypium hirsutum*. This non-uniformity was related to the geographical restriction on vector activity already referred to, but the data indicate that the restriction was not a simple function of distance alone. In addition to distance, the shape of the area occupied by the population entered in and rather radically altered the vector-plant interaction.

It is pertinent at this point also to refer to the observations of Kobel (243). A transfer of pollen within the beehive was observed, resulting in potential pollination over greater distances than would otherwise have occurred.

2. Geographic and Climatic Influences

Various geographical factors may influence the breeding method of a particular species. It is commonly observed that the breeding system varies from one geographical location to another, but it is not always easy to define what variable is responsible for this variation. Temperature, humidity, precipitation, other organisms might all be involved. Jones and Newell (218) present data showing the influence of certain environmental factors on floral behavior in grasses. The effect of these influences on the breeding system, however, is not indicated. It will suffice to present a few examples of such environmentally induced variation, together with the general conclusion that information concerning the breeding method of a particular species in one locality need not be correct for the same species elsewhere.

Scandinavian biotypes of *Deschampsia caespitosa*, which are fully sexual in their native habitat, reproduce by facultative vivipary when transferred to California (150). Native biotypes of this species in California only rarely reproduce viviparously (184). The exact geographic and climatic factors eliciting this response are not clear, but the greater aridity of the California habitat is considered suggestive (150).

The per cent natural crossing in *Gossypium hirsutum* varies quite widely with geographical locality (389). Reported figures range from a negligible quantity (1 or 2%) to amounts in excess of 50%. In this instance it seems valid to equate this geographic variation directly to variation in insect populations which are agents of pollen distribution for *Gossypium*. These insect populations vary geographically, largely perhaps in response to variations in precipitation.

Rick (362) has presented information on the variation in breeding method of *Lycopersicon esculentum* due to geographical location. This species, in its native habitat (Peru), exhibits an appreciable amount of natural crossing; in other areas of the world, where it has been introduced subsequently as a cultigen (North

America, Europe, etc.), it is essentially autogamous. This variation arises from the presence of suitable insect pollinators in Peru, which are absent elsewhere.

Lespedeza cuneata and other species of *Lespedeza* possess two types of flowers: chasmogamous petaliferous and cleistogamous apetalous. The latter are, of course, entirely self-pollinated, while the former exhibit about 70% natural crossing. The total amount of natural crossing shown by this species, then, depends upon the relative proportions of the two types of flowers. Since these relative proportions are subject to environmental influence (284), it is apparent that the breeding method will change in response to changes in the appropriate environmental conditions.

Suneson (423) has indicated that the advent of frost will initiate natural crossing in *Hordeum vulgare* which is generally a self-pollinator. This effect provides a temporal variation of the breeding method within the season.

The preceding examples serve to suggest cautions to be observed in interpreting information on breeding methods. More important, perhaps, they serve to suggest the dangers of extrapolating information obtained under one set of conditions to a different situation.

3. Genetic Influences

Similar cautions might be suggested on a genetic basis. That is, the genotype is known to influence directly the rate of natural crossing in numerous cases, and such a genetic differential must be considered as existing potentially in any species. Such a genetic influence may be as obvious and as genetically simple as the gene reported by Rick (360) in *Lycopersicon esculentum*. This gene suppresses the development of hairs and specifically causes absence of the hairs which normally hold the anthers together in a column or tube closely surrounding the style. Thus the absence of these hairs, a morphologically simple change, has a marked effect on natural crossing through removing the anthers from their direct proximity to the stigma and thus in reducing the proportion of self-pollination in plants of this genotype. The causal relationships here are easily traced.

More commonly, however, the relationships are less easily established, and the differences, though indisputably present, are

more subtle and may be defined only obscurely. These may relate to such relative intangibles as insect preference, or they may actually show evidence of an interaction of genotypes with location (environments), a not unexpected possibility. Finkner (120) presents data suggesting that such an interaction was found in the material (*Gossypium hirsutum*) which he studied.

As a few examples of varietal differences within a species in rate of natural crossing, the following species are cited: *Gossypium hirsutum* (120, 390), *Phaseolus lunatus* (6), *P. vulgaris* (27), *Lupinus luteus* (152), *Cocos nucifera* (267), *Pisum sativum* (172b).

Another possible genetic influence on crossability is indicated by Straub (419) who found that changes in ploidy level affect not only the size of the flower but also its form—that is, the relative size of its parts. In addition, anther positioning is influenced. These differences will likely have an influence on the mode of pollination of the plant and will thus be adaptive in terms of selection for the more advantageous breeding system. This facet of the relation of polyploidy to the evolution of plant species merits further investigation.

Most of the preceding examples of the influence of genotype on natural crossing are concerned with morphological and temporal changes in the floral mechanism: changes in the positioning or relative size of floral parts, changes in the rate of blooming, or in the timing of anthesis, perhaps changes in the relative attractiveness to pollinators, etc. These factors are all concerned with pollination, the transfer of pollen to the stigma. It must be recognized, however, that the subject of this review is pollination only indirectly; this review is directly concerned with fertilization or syngamy. Pollination and fertilization will generally be equivalent. Where differential fertilization follows pollination (through differential pollen tube growth, for example), the two will not be equivalent. It is evident that, from our present orientation, fertilization is the phenomenon of interest, and that pollination, should it differ as a result of pollen selectivity (see 217), is merely incidental. This serves, then, as a reiteration of the criticism offered in the Introduction of the older "morphologic" approach to reproductive behavior. A mere consideration of the structure and apparent adaptation for pollination of the flower of a species

may be quite misleading; only by experimental assessment of the proportion of self- and cross-fertilization, by the methods reviewed here, can a knowledge of the breeding system be gained.

In the literature the words "pollination" and "fertilization" are frequently used somewhat interchangeably, since they are commonly equivalent in outcome. It should be clear that, rigorously, "fertilization" is the exact word and that "pollination" may or may not have an equivalent meaning from the genetic viewpoint. The extreme case, of course, is found with self-incompatibility, where a plant may be regularly self-pollinated but never self-fertilized. Usage should be exact and consequently should (and in this review does) distinguish between these two phenomena, where such a distinction is pertinent.

4. Experimental Modification of the Breeding System

Self-incompatibility has been implied to be an immovable barrier in the breeding systems of plants exhibiting this phenomenon. In practice it has been possible to circumvent this barrier and experimentally to achieve autogamy under appropriate circumstances. For example, Eyster (113) has shown that chemical treatment of a self-sterile plant is capable of rendering it fertile to its own pollen. Stout (416) reviews various kinds of variability in incompatibilities. These include: experimental manipulations such as style transplanting and washing away of stigmatic secretions; end-of-season fertility, which occurs in some self-incompatible plants just before the cessation of reproductive activity for the season; bud fertility, wherein self-pollination may be accomplished by pollinating an immature pistil with mature pollen.

Other experimental methods of changing the breeding system are also available. For example, Wittwer and Hillyer (472) describe experiments in which the normally monoecious *Cucurbita pepo* was made male-sterile (that is, the staminate flowers were completely inhibited) by treating the seedlings with maleic hydrazide. Thus complete outcrossing was achieved.

5. Influence of Selection

Under the heading of factors which influence reproductive behavior must be mentioned the influence of selection, i.e., the adaptive value of different breeding systems. Under the impact

of selection a species may alter its breeding system as an adaption to a changing environment. This phenomenon has apparently been observed in *Primula vulgaris* (83). Harland (170) suggests how selection for rate of pollen tube growth would result in a fully autogamous variety and describes a method whereby this might be accomplished.

It was suggested in the Introduction that the widespread occurrence of sexuality in the biological world argues for the adaptive value of genetic variability. Furthermore, the prevalence of self-incompatibility and other outbreeding mechanisms substantiates this view. Perhaps such a statement elaborates the obvious. Why, then, do autogamous and apomictic forms persist? Obviously, other factors are operating. For example, in the Arctic various types of apomixis enable plants to propagate where the season is too short to allow development of flowers, fruits and seeds (337). Self-pollination (also apomixis) allows of more certain seed production, though at a sacrifice of genetic variability, and may be of adaptive value where conditions are such as to limit cross-pollination. Such conditions might be encountered when there is a dearth of pollen vectors (155) or where plants are spaced at such wide intervals that cross-pollination is restricted. The adaptive value of self-compatibility and consequent initial autogamy in its relation to establishment after "long distance dispersal" of self-incompatible plants has been pointed out by Baker (21). If such dispersal over great distance, resulting in a discontinuous distribution, is accomplished by a few seeds or even a single propagule, the subsequent establishment or failure of the new colony may depend upon whether self-compatibility or incompatibility is found. Thus a very rigorous selective screen may be provided in some circumstances.

V. EXPLANATION OF TABULATION

The following tabular data comprise a compilation of such information concerning the reproductive behavior of phanerogams as could be gleaned from the literature. Previous compilations of this sort (180, 213, 343, 172b) have been limited in scope and in some cases inadequately substantiated. In this compilation appropriate citations are given in each case. Some of these citations

represent detailed studies of an exacting nature giving highly specific information concerning reproductive behavior; others represent deductions concerning reproductive behavior based on indirect evidence; still others are little more than casual observations and can merely be construed as suggestive of the mode of reproduction which actually exists. Consequently it is urged that the reader who is interested in a particular species or group refer to the original citations in order to see the original data (if any) and to evaluate the evidence presented. The accompanying tabulation, then, can claim only partially to be descriptive; its more important aim is to serve as a key to the literature.

The attempt is made to include in this tabulation information about as many species of plants as possible. An attempt was not made to include all literature citations which were related to reproductive behavior in plants. That is, this compilation does not claim to be bibliographically exhaustive, though it endeavors to be biologically exhaustive. For example, a wealth of citations concerning natural crossing could be presented for most of the more important cereal grasses, since these economically important grasses have been extensively studied in numerous parts of the world. In such cases, only selected references are cited. These have been chosen on the basis of one or more of the following points: (*a*) having the most convincing evidence, (*b*) having ample literature citations, and thus being keys to the literature for the species concerned, or (*c*) being found in more readily available journals. It has not been possible to meet all these criteria in all cases.

It is recognized, of course, that although this compilation attempts to be complete, it is, in fact, not so. Therefore the reader is requested to communicate with the author and to supply him with additional information which could be used in an amplification of this list. Citations of published material which have been overlooked in this review, citations of unpublished information, and corrections of improper citation will all be welcomed.

It is noteworthy that in only a relatively few cases, designated by ***, have disagreements concerning a particular species been encountered. These disagreements may have resulted from uncritical work by the investigators concerned or from the fact that

the several investigators were actually dealing with different material. A resolution of such discrepancies will be of particular interest to workers dealing with these species.

The following form has been used in presenting the material. The breeding behavior of a particular species or subdivision thereof may be represented as a point on an equilateral triangle (see Figure 1), the apices of which represent complete self-fertilization,

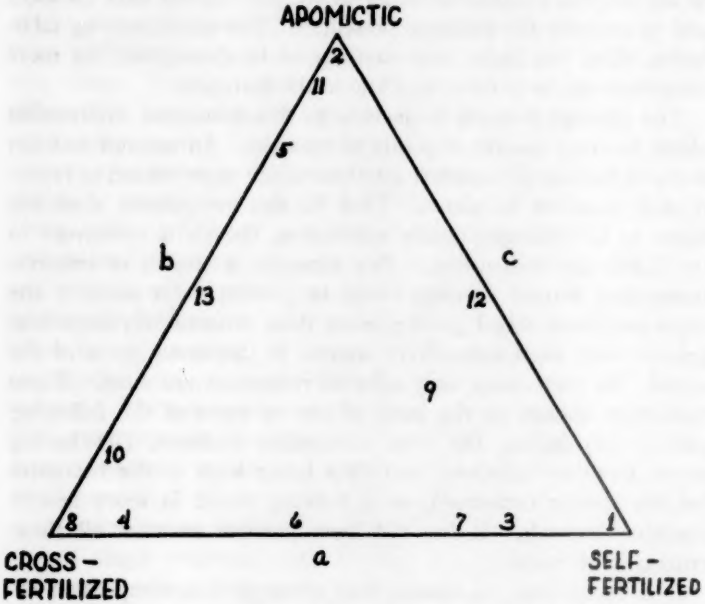

FIG. 1. The "reproductive triangle", a diagrammatic representation of the reproductive method of various species.

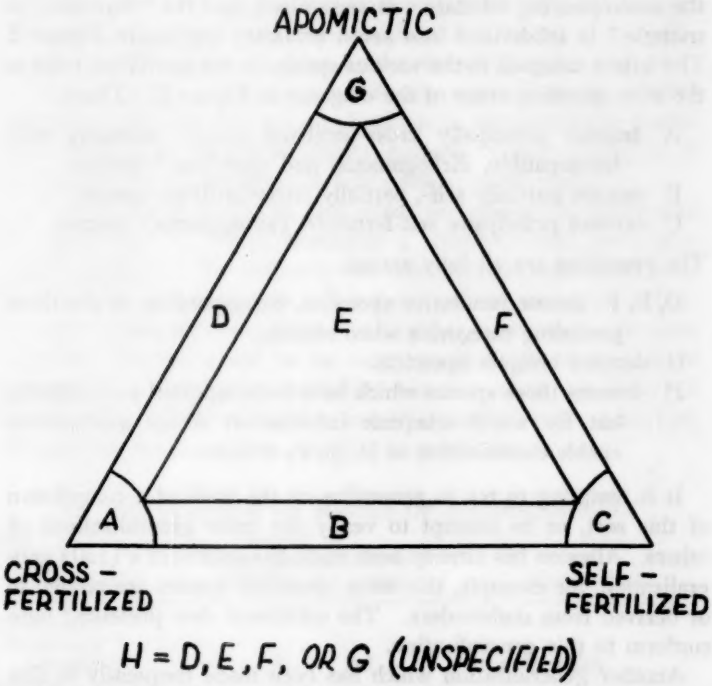

FIG. 2. A simplification of the "reproductive triangle" into seven general regions.

complete cross-fertilization, and obligate apomixis. All fully sexual species will lie somewhere on side "a" of the triangle, depending on the proportions of self- and cross-fertilization which are found. Gustafsson (150) has pointed out that most apomicts are cross-fertilizers when sexual. Hence the majority of apomicts will be found on side "b" of the triangle. Side "c" and the interior of the triangle will be relatively unoccupied. Figure 1 indicates the location on such a diagram of several representative species.

As seems evident, a species can be exactly located on such a diagram only if fairly extensive data are available. Generally this is not the case, and the particular species can be assigned only an approximate position in the diagram. This difficulty in

the accompanying tabulation is recognized, and the "reproductive triangle" is subdivided into seven arbitrary regions in Figure 2. The letters assigned to the various species in the tabulation refer to the corresponding areas of the diagram in Figure 2. Thus:

A denotes principally cross-fertilized plants, including self-incompatible, dichogamous, and dioecious * species.
B denotes partially self-, partially cross-fertilized species.
C denotes principally self-fertilized (autogamous) species.

The preceding are all fully sexual.

D, E, F denote facultative apomicts, corresponding to the three preceding categories when sexual.
G denotes obligate apomicts.
H denotes those species which have been reported as apomictic, but for which adequate information is not available to enable classification as D, E, F, or G.†

It is tempting to try to generalize on the basis of a compilation of this sort, or to attempt to verify the prior generalizations of others. Allusion has already been made to Gustafsson's (150) generalization, for example, that most apomictic species are related to or derived from outbreeders. The additional data presented here conform to this generalization.

Another generalization which has been made frequently is that most or all forest trees are cross-pollinators. Examples of fully autogamous trees are lacking in this survey, and this generalization is probably valid. However, it must be pointed out that data are available for only a relatively limited number of species in this category. This, of course, is largely due to the inherent difficulty of obtaining data from plants with such prolonged life cycles.

Rather than to attempt to formulate new and additional generalizations, it is considered more in keeping to suggest why such attempts should be made with great caution. The question is principally one of sampling. The species listed here cannot be considered as a random sample of phanerogams. For example,

* Dioecism is generally mentioned in taxonomic descriptions, and a complete listing of all dioecious species is impossible. Only a few are included here, usually those having some particular (generally economic) interest.

† Apomixis is used here to include all forms of non-sexual reproduction in phanerogams (see Gustafsson (150)). These include such vegetative methods of propagation as runners and bulbils, in addition to the more specialized processes of agamospermy.

cultivated and otherwise economically important species are disproportionately represented. One might argue, rightly or wrongly, that cultivated plants are more commonly autogamous than non-cultivated plants. Hence any conclusion concerning the relative proportions of self- and cross-pollination in any particular family represented here would be highly suspect. Other examples of disproportionate representation will come to mind readily.

Finally a word should be said about the taxonomic identity of the species listed herein. Generally a reference cited for a particular species is the authority for the further identification of the material concerned. In a few cases, where synonymy exists, the most commonly recognized binomial has been listed. In such cases the binomial given in the reference is listed afterwards in parentheses. Commonly available manuals, such as those of Bailey (15), Hitchcock (184) and Weintraub (463), constitute the basis for the taxonomic grouping in most cases.

VI. TABULATION OF MODES OF REPRODUCTION

Family Genus Species	Mode of Reproduction (See Fig. 2)	Reference	Comments
ACANTHACEAE			
Thunbergia			
grandiflora	A	104	Self-incompatible
ACERACEAE			
Acer			
buergerianum	A	473a	Dichogamous
campestre	B	335	Probably
ginnala	B	335	Probably
japonicum	A	473a	Dichogamous
negundo	A	161	Dioecious
palmatum	A	473a	Dichogamous
platanoides	A	335, 473a	Self-incompatible
pseudo-platanus	B	335	Probably
pseudosieboldianum	B	335	Probably
rubrum	B	335	Probably
saccharinum	A	335	Self-incompatible
saccharum	B	473a	Natural selfing probable, although tends to dioeciousness
spicatum	A	335	Self-incompatible
tataricum	A	335	Self-incompatible
tegmentosum	A	335	Self-incompatible
AGAVACEAE			
Agave			
americana	A	104, 150	In native habitat (Centr. Amer.)
	G		In Mediterranean area; sterile due to lack of a pollinator but spreading vegetatively

Family Genus Species	Mode of Reproduction (See Fig. 2)	Reference	Comments
AGAVACEAE (cont.)			
Agave (cont.)			
angustifolia	D	150	
calodonta	A	150	Self-incompatible
candelabrum	H	150	
cantula	H	150	
ferox	A	104	Self-incompatible
fourcroydes	H	150	
franceschiana	G	150	
lespinassei	H	150	
littaeoides	A	150	Self-incompatible
lurida	H	150	
miradorensis	G	150	
salmiana	H	150	
sisalina	G	449, 150	
vivipara	H	150	
watsoni	A	150	Self-incompatible
zapupe	H	150	
Phormium			
tenax	C	198	
Sansevieria			
thrysiflora (*guineensis*)	G	222, 223	Produces no seed, though pollen appears normal
trifasciata	A	222	
Yucca spp.		460	
aloifolia	A	104	Self-incompatible
arizonica	A	460	Self-incompatible (some self-compatibility)
elata	A	460	Self-incompatible (some self-compatibility)
smalliana (*filamentosa*)	A	104	Self-incompatible
neomexicana	A	460	Self-incompatible (some self-compatibility)
reverchoni	A	460	Self-incompatible (some self-compatibility)
thompsoniana	A	460	Self-incompatible
treculeana	A	104	Self-incompatible
AMARYLLIDACEAE			
Allium			
amplectens	H ?	150	
ascolonicum	H	150	
a. var. Homer Red	G	235	
carinatum	G	150	
cepa	A	266, 444, p. 239	About 93% natural crossing
moly var. *bulbiferum*	G	150	Seed formation can be induced
multibulbosum	D	150	Self-incompatible
nutans	A	257	Self-incompatible (some self-compatibility)
ramosum (*odorum*)	G	150	
oleraceum	G	150	
paradoxum	G	150	
proliferum	H	150	
roseum var. *bulbiferum*	H	150	
sativum	G	444, p. 248	

Family Genus Species	Mode of Reproduction (See Fig. 2)	Reference	Comments
AMARYLLIDACEAE (cont.)			
Allium (cont.)			
schoenoprasum	A	257	Self-incompatible
scorodoprasum	G	150	Seed formation can be induced
vineale	G	150	
viviparum	H	150	
zebdanense	G	150	
Alstroemeria			
haemantha	A	442	Dichogamous
psittacina	A	442	Dichogamous
pulchra	A	442	Dichogamous
Cooperia			
pedunculata	H	314	
Curculigo			
capitulata (*recurvata*)	A	104	Self-incompatible
Cyanella			
capensis	C	332	
Fourcroya			
cubensis	G	150	
gigantea	H	150	
Hymenocallis			
occidentalis	A	104	Self-incompatible
Hypoxis			
hirsuta	A	104	Self-incompatible
Narcissus			
incomparabilis	G	150	
jonquila	A	219	
triandrus	A	29	Self-incompatible
Nothoscordum			
fragrans	H	160	
Zephyranthes			
atamasco	A	314	Self-incompatible
caudata	A	314, 150	Self-incompatible
grandiflora (*carinata*)	A	314	Self-incompatible
texana	H	150	
ANACARDIACEAE			
Mangifera			
indica	E	150, 305, 188	
Pistacia			
vera	A	62	Dioecious
Rhus			
vernicifera	A	327	Dioecious
Spondias			
purpurea	—	224	Microgametogenesis fails to occur
ANNONACEAE			
Annona			
cherimola	A	105, 383	
APOCYNACEAE			
Allamanda			
blanchetii	A	104	Self-incompatible
cathartica			
var. *grandiflora*	A	104	Self-incompatible
var. *hendersonii*	A	104	Self-incompatible

Family Genus Species	Mode of Reproduction (See Fig. 2)	Reference	Comments
APOCYNACEAE (cont.)			
Amsonia			
tabernaemontana	H ?	150	
Beaumontia			
grandiflora	A	104	Self-incompatible
Nerium			
oleander	A	104	Self-incompatible
Odontadenia			
grandiflora	A	104	Self-incompatible
Tabernaemontana			
echinata	A	104	Self-incompatible
Vinca			
major	A	104	Self-incompatible
minor	A	104	Self-incompatible (some self-compatibility)
rosea	A	381	Self-incompatible
AQUIFOLIACEAE			
Ilex			
aquifolium	A	367	Dioecious
ARACEAE			
Acorus			
calamus	G	150	
Amorphophallus			
oncophyllus	H	150	
Arum			
italicum	A	17	Self-incompatible
Colocasia			
esculenta	B	444, p. 311	
Spathiphyllum			
patinii	H	150	
Symplocarpus (*Spathyema*)			
foetidus	A	414	Dichogamous
Zantedischia			
aethiopica	A	137	Dichogamous
ARALIACEAE			
Panax			
schin-seng	B	426	10 to 27% natural crossing
quinquefolius	A	—	Dioecious to polygamous
ARISTOLOCHACEAE			
Aristolochia spp.	A	141	Dichogamous
Asarum			
canadense	C	467	
europaeum	C	247	
ASCLEPIADACEAE			
Asclepias			
subulata	A	38	Self-incompatible
syriaca (*cornutii*)	A	338, 400	Self-incompatible
Cryptostegia			
grandiflora	A	425	
madagascariensis	A	425	
Hoya			
carnosa	A	104	Self-incompatible
BALANOPHORACEAE			
Balanophora			
globosa	H	150	
japonica	H	150	

Family Genus Species	Mode of Reproduction (See Fig. 2)	Reference	Comments
BALANOPHORACEAE (cont.)			
Juelia			
subterranea	H ?	150	
BALSAMINACEAE			
Impatients			
fulva	B	58	Both cleistogamous and chasmogamous flowers are found; both fertile
BETULACEAE			
Alnus sp.	A	138	Dichogamous
serrulata (*rugosa*)	G	473	
Betula sp.	A	138	Dichogamous
Corylus			
avellana	A	148	Dichogamous
BIGNONIACEAE			
Tabebuia			
serratifolia	A	104	Self-sterile
Tecomaria			
capensis	A	104	Self-incompatible
BOMBACACEAE			
Ceiba			
pentandra var. *indica*	C or B	440, 202	Self-pollinated in Java; partially outcrossed in Africa
Pachira			
aquatilis	H	22	Adventitious embryony
insignis	A	104	Self-incompatible
BORAGINACEAE			
Borago			
officinalis	A	104	
Symphytum			
bulbosum	A	104	Self-incompatible
BROMELIACEAE			
Ananas			
comosus (*sativus*)	A	104, 70	Self-incompatible
Billbergia			
speciosa	A	104	Self-incompatible
BURMANNIACEAE			
Burmannia			
candida	C	150	
championii	C	150	
coelestis	H	150	
disticha	C	150	
Thismia			
javanica	H ?	150	
BURSERACEAE			
Canarium			
ovatum	A	63	Dioecious
BUTOMACEAE			
Butomus			
umbellatus	A	141	Dichogamous
BUXACEAE			
Sarcococca			
hookeriana	H	150	
h. var. *humilis* (*humilis*)	H ?	150	
pruniformis	H	150	

Family Genus Species	Mode of Reproduction (See Fig. 2)	Reference	Comments
BUXACEAE (cont.)			
Sarcococca (cont.)			
ruscifolia	H	150	
zeylanica	H	150	
Simmondsia			
chinensis	D ?	139	Dioecious (apomixis probable)
CACTACEAE			
Opuntia			
aurantiaca	H	150	
ficus-indica	H	150	
glaucophylla	H ?	150	
leucantha	H	150	
rafinesquii	H	150	
tortispina	H ?	150	
CALLITRICHACEAE			
Callitriche			
hamulata	B	104	
CALYCANTHACEAE			
Calycanthus			
fertilis	H ?	150	
floridus	H ?	150	
occidentalis	H ?	150	
CAMPANULACEAE			
Adenophora spp.	H ?	314	
Campanula			
persicifolia	A	133	Self-incompatible (self-compatibility found in tetraploid forms)
rotundifolia	A	18	
Michauxia			
campanuloides	A	259	Self-incompatible
Platycodon			
grandiflorum	A	414	Dichogamous
CAPPARIDACEAE			
Capparis			
frondosa	H	150	
Isomeris			
arborea	G	43	
CAPRIFOLIACEAE			
Viburnum			
carlesii	A	104	Self-incompatible
CARICACEAE			
Carica			
papaya	A (C)	163, 411	Dioecious, but with hermaphroditic individuals which are autogamous. See 411 for genetics of sex-determination
CARYOPHYLLACEAE			
Arenaria			
ciliata	A	298	Probably
gothica	A	298	Probably
leptoclados	C	298	
norvegica	A	298	Probably
serpyfolia	C	298	

Family Genus Species	Mode of Reproduction (See Fig. 2)	Reference	Comments
CARYOPHYLLACEAE (cont.)			
Cerastium			
alpinum	A	298	
arvensis	A	298	
brachypetalum	C	298	
cerastioides	A	298	Probably
edmonstoni	A	298	
glomeratum	C	298	
pumilum	C	298	
regelii	H ?	150	
semidecandrum	C	298	
tetrandrum	C	298	
tomentosum	A	298	
vulgatum	C	298	
Corrigiola			
litoralis	C	298	
Dianthus			
caryophyllus	B	290	Apparently, since individual flower dichogamous but self-fertile
Honckenya			
peploides	H ?	122	
Lychnis			
coeli-rosa (*Viscaria oculata*)	A	436	
flos-cuculi	A	219	Dichogamous
Melandrium			
album	A	22	Dioecious
macrocarpum	A	22	Dioecious
noctiflorum	C	22	
rubrum (*dioicum*)	A	22	Dioecious
Minuartia			
verna	A	298	
Moehringia sp.	B	298	
Moenchia			
erecta	C	298	
Polycarpon			
tetraphyllum	C	67 (cited by 22)	
Sagina spp.	C	298	
Scleranthus			
annuus	C	67 (cited by 22)	
perennis	C	67 (cited by 22)	
Silene			
acaulis	A	22	Imperfectly dioecious
conica	C	22	
cucubalus	A	22, 219	Imperfectly dioecious
Spergula			
arvensis	C	114	
longipes	C	298	
sativa	C	298	
vernalis	C	298	

Family Genus Species	Mode of Reproduction (See Fig. 2)	Reference	Comments
CARYOPHYLLACEAE (cont.)			
Spergularia			
bocconei	C	298	
marginata	B	298	
rupicola	A	298	
rubra	C	298	
salina	C	298	
Stellaria			
alsine	C	298	
apetala	C	298, 150	
crassipes (longipes)	G	150	
holostea	B	298, 219	
media	C	173	
neglecta	C	150, 298	"Perhaps sometimes cross-pollinated" also (298)
CELASTRACEAE			
Celastrus			
scandens	D or G	150	Dioecious, when sexual
Euonymus			
americanus	H ?	150	
europaeus	D ?	150	
latifolius	H	150	
CHENOPODIACEAE			
Atriplex			
ca. 16 annual spp. from Australia	B	196	"Monoecious . . . capable of self-pollination . . . probably cross-pollinate freely"
Perennial spp. from Australia (Including: *A. nummularium*, *A. paludosum*, *A. stipitatum*, *A. vesicarium*, *A. cinereum*, and *A. rhagodioides*)	A	196	Largely dioecious
Beta			
vulgaris	A	64, 324	Self-incompatible (self-compatibility also found)
Haloxylon			
ammodendron	A	44	
Kochia			
georgii	A	196	Dichogamous
Spinacia			
oleracea	A	39, 432	Dioecious; inbred monoecious lines exhibit 20–97% natural crossing
COMMELINACEAE			
Commelina			
benghalensis	C	104	
Floscopa spp.	C	298	
COMPOSITAE			
Achillea			
millefolium	A	462	Self-incompatible

Family Genus Species	Mode of Reproduction (See Fig. 2)	Reference	Comments
COMPOSITAE (cont.)			
Antennaria			
alpina	H	150	
brainerdii	H	150	
canadensis	H	150	
carpatica	H	314	
dioica (in part)	H	404	
fallax	H	150	
glabrata	H	150	
groenlandica	H	150	
intermedia	H	150	
magellanica	H	150	
neodioica	H	150	
occidentalis	H	150	
parlinii	H	150	
petaloidea	H	150	
porsildii	H	314	
Arnica			
alpina	H	150	
chamissonis	H	150	
diversifolia	H	150	
Artemesia			
nitida	G	150	
Aster			
amethystinus	A	104	Self-incompatible
ericoides	A	104	Self-incompatible
laevis	A	104	Self-incompatible
linariifolius	A	104	Self-incompatible
novae-angliae	A	104	Self-incompatible
novi-belgi	A	104	Self-incompatible
patens	A	104	Self-incompatible
puniceus	A	104	Self-incompatible
shortii	A	104	Self-incompatible
tataricus	A	104	Self-incompatible
turbinellus	A	104	Self-incompatible
Bellis			
perennis	C	219	
Callistephus (*Callistemma*)			
chinensis	B	471	10% natural crossing
Carthamus			
oxycantha	A	95	
tinctorius	B	227, 66	
Centaurea			
cyanus	G	150	
jacea	A	18	
Chondrilla			
acantholepis	H	150	
ambigua	A	150	Self-incompatible
brevirostris	H	150	
coronifera	H	150	
graminea	H	150	
juncea	H (G ?)	150	
kouznezowii	H	150	
lejosperma	H	150	

Family Genus Species	Mode of Reproduction (See Fig. 2)	Reference	Comments
COMPOSITAE (cont.)			
Chondrilla (cont.)			
ornata	H ?	150	
pauciflora	H	150	
Chrysanthemum			
cinerariaefolium	A	435	Self-incompatible
indicum	A	429	Self-incompatible in tetraploid forms; slight self-compatibility in hexaploid forms
japonense	A	429	Self-incompatible (slight self-compatibility)
makinoi	A	429	Self-incompatible
morifolium	A	299	Self-incompatible (some self-compatibility occurs)
ornatum	A	429	Self-incompatible (slight self-compatibility)
pacificum	A	429	Self-incompatible (slight self-compatibility)
shiwogiku	A	429	Self-incompatible (slight self-compatibility)
wakasaense	A	429	Self-incompatible
Cichorium			
endivia	B	28	15% natural crossing
intybus	A	412	Self-incompatible (some self-compatibility)
Coreopsis			
pubescens	A	159a	Self-incompatible
tinctoria (*bicolor*)	D	100, 150	Self-incompatible (slight self-compatibility) with low rate of apomixis
verticillata	A	159a	Self-incompatible
Cosmos			
bipinnatus	A	85	Self-incompatible
Crepis			
acuminata (in part)	H	150	
bakeri (in part)	H	150	
barbigera	G	150	Probably obligate
capillaris	A	22, 69	Self-incompatible
exilis (*atribarba*) (in part)	H	150	
foetida ssp. *rhoeadifolia*	A	195	Self-incompatible
intermedia	H	150	
modocensis (in part)	H	150	
monticola (in part)	H	150	
occidentalis (in part)	H	150	
paludosa	A	22	Self-incompatible
pleurocarpa (in part)	H	150	
Dahlia			
sp. (*pinnata*?)	A	104, 252	Self-incompatible
Erigeron			
annuus	G	281, 115	
karwinskianus var. *mucronatus*	G	33, 115	

Family Genus Species	Mode of Reproduction (See Fig. 2)	Reference	Comments
COMPOSITAE (cont.)			
Erigeron (cont.)			
ramosus	H	150	
strigosus	G	281	
Eupatorium spp.	H	145	Several triploid species are probably apomictic
cannabinum	A	185	Self-incompatible
glaberrimum	A	185	Self-incompatible
glandulosum	H	145, 185	
ligustrinum (*weinmannianum*)	A	185	Self-incompatible
petiolatum	A	185	Self-incompatible
purpureum	A	185	Self-incompatible
purpusi	A	185	Self-incompatible
rugosum (*ageratoides*)	A	185	Self-incompatible
sordidum (*ianthinum*)	A	185	Self-incompatible
Guizotia			
abyssinica	A	190	
Helianthus			
annuus	B or A	450, 348, 231	Two strains showed 62% and 17% natural crossing; some self-incompatibility also found
cucumerifolius	A	450	Self-incompatible (some self-compatibility found)
macrophyllus	A	450	Self-incompatible
rigidus	A	450	Self-incompatible
tuberosus	A	450	Self-incompatible (some self-compatibility found)
Helichrysum			
bracteatum	A	87a	Self-incompatible
Hieracium			
subgenus *Euhieracium* (excepting *H. speciosum*, *H. bifidum*, *H. transsylvanicum*, *H. albidum*, *H. umbellatum*, *H. sparsum* and *H. virgaurea*, which are sexual)	G	150	
subgenus *Pilosella* (excepting *H. auricola*, *H. pavichii*, which are sexual)	D	150	
auricola	A	150	Self-incompatible
umbellatum	A	150, 18	Polyploid apomicts occur
Hypochaeris			
radicata	A	22	Self-incompatible
Ixeris			
dentata	G	150	

Family Genus Species	Mode of Reproduction (See Fig. 2)	Reference	Comments
COMPOSITAE (cont.)			
Lactuca			
sativa	C	433	2½% natural crossing
Launaea			
asplenifolia	A	104	Self-incompatible
Leontodon			
autumnalis	A	18	
hispidus	D	150	Apomixis rare
Parthenium			
argentatum	G	150	High chromosome numbers
	A		Low chromosome numbers (self-incompatible)
incanum (in part)	H	150	
Picris			
echioides	A	22	Self-incompatible (self-compatible races also)
hieracioides	D	150, 22	Self-incompatible (apomixis rare)
Rudbeckia			
californica	H	314	
deamii	H	314	
hirta	A	104	Self-incompatible
laciniata (in part)	H	32	
speciosa	H	150	
sullivanti	H	314	
triloba	H	314	
Scorzonera			
tau-saghys	A	340	Self-incompatible
Senecio			
cruentis	A	104	Self-incompatible
viscosus	A	22	Self-incompatible
vulgaris	B	175	
Solidago			
asperula	A	104	Self-incompatible
canadensis	A	104	Self-incompatible
cutleri (*virgaurea*)	B	22	
drummondii	A	104	Self-incompatible
racemosa	A	104	Self-incompatible
rugosa	A	104	Self-incompatible
sempervirens	A	104	Self-incompatible
Sonchus			
tenerrimus	A	104	Self-incompatible
Tagetes			
erecta	A	312	Probably
patula	A	312	Probably
Taraxacum			
bessarabicum	C	150	
calcarum	H	150	
duplidens	A	104	Self-incompatible
karatavicum	A	150	Self-incompatible (probably)
kok-saghyz	A	453, 454, 221	Warmke concludes: ordinarily self-sterile, but when peak seed-set occurs, it results from selfing

Family Genus Species	Mode of Reproduction (See Fig. 2)	Reference	Comments
COMPOSITAE (cont.)			
Taraxacum (cont.)			
megalorrhizon	H (G ?)	197	
multiscaposum	A	150	Self-incompatible
obtusilobum	A	150	Self-incompatible
officinale	G	74	
platycarpum	A	150	Self-incompatible
serotinum	A	150	Self-incompatible
Townsendia			
anomala	A	37	Self-incompatible
arizonica	A	37	Self-incompatible
florifera	A	37	Self-incompatible (some self-compatibility)
incana	H	37	
minima	H	37	
montana	H	37	Tetraploid forms
	A		Diploid forms (self-incompatible)
parryi	H	37	Tetraploid forms
	A		Diploid forms (self-incompatible)
Tussilago			
farfara	A	219	
Zinnia			
elegans	A	104	Self-incompatible
CONVOLVULACEAE			
Ipomoea			
batatas	A	437, 341	Self-incompatible
nil (*Pharbitis nil*)	B	159, 232	4% to 25% natural crossing
pes tigridis	C	104	
CRUCIFERAE			
Aethionaema			
grandiflorum	A	104	Self-incompatible
Arabis			
holboelii var. *typica*	H	314	
Armoracia			
lapathifolia (*rusticana*)	A	410, 477	Extremely low seed-set, some male-sterility
Brassica			
campestris	A	191, 320	Self-incompatible
chinensis	A	413	Self-incompatible (some self-compatibility)
hirta (*Sinapis alba*)	A	34	
juncea	A	477, 191	Self-incompatible; self-compatible types also
napobrassica	B	259	25% natural crossing
napus	B	304, 172b	10% natural crossing
oleracea	A	330, 11, 296, 477	Largely self-sterile; 50% natural crossing observed in a self-fertile clone
pekinensis	A	413	Self-compatible (some self-compatibility)
rapa	A	191	Self-incompatible

Family Genus Species	Mode of Reproduction (See Fig. 2)	Reference	Comments
CRUCIFERAE (cont.)			
Capsella			
bursa-pastoris	C or A	18, 150	All tetraploid and some diploid forms C, other diploid forms self-incompatible
grandiflora	A	365	
occidentalis (*Bursa occidentalis*)	C	18	
Cardamine			
bulbifera	D	104, 150	Self-incompatible when sexual, but sexuality rare
pentaphylla	A	150	Self-incompatible
pinnata	A	150	Self-incompatible
polyphylla	A	150	Self-incompatible
pratensis	A or H	104, 385, 150	Self-incompatible; apomictic in arctic
Cheiranthus			
cheiri	C ?	219	
Cochlearia			
danica	C	150	
Crambe			
tatarica	A	104	Self-incompatible
Erophila			
verna	C	18	
Eruca			
sativa	A	4	Self-incompatible
Hesperis			
tristis	A	104	Self-incompatible
Hugueninia			
tanacetifolia	A	104	Self-incompatible
Iberis			
amara	A	31	Self-incompatible (self-compatibility found in cultivated races)
pinnata (*affinis*)	A	104	Self-incompatible
Lobularia			
maritima	A	104	Self-incompatible
Mathiola			
incana var. *annua* (*Matthiola annua*)	C	312	
Raphanus			
raphanistrum	A	104, 477	Self-incompatible (some self-compatibility)
sativus	A	82	86 to 100% natural crossing; self-incompatibility found
Subularia			
aquatica	C	104	
CUCURBITACEAE			
Citrullus			
vulgaris	B	294	
Cucumis			
melo	B	466	
sativus	B	207	65 to 70% natural crossing

Family Genus Species	Mode of Reproduction (See Fig. 2)	Reference	Comments
CUCURBITACEAE (cont.)			
Cucurbita spp.	A	278	Presumably *C. maxima*, *C. moschata*, and *C. pepo*
Luffa			
acutangula	A	359	A - - - : monoecious aaB - : female aabb : hermaphroditic
Tricosanthes			
dioica	A	391	Dioecious
CYPERACEAE			
Carex			
paludosa	A	219	Dichogamous
Eleocharis			
rostellata	H	252	
Eriophorum			
angustifolium (*polystachion*)	G	333	
DIPSACACEAE			
Knautia			
arvensis	H ?	252a	
Succisa			
pratensis	A	18	
DROSERACEAE			
Aldrovandia			
vesiculosa	C	104	
EBENACEAE			
Diospyros			
kaki	A	62	Variably dioecious
virginiana	A	62	Dioecious
ELEAGNACEAE			
Hippophaë			
rhamnoides	A	89	Dioecious (hermaphrodites known)
ERICACEAE			
Andromeda			
polifolia	C	158	
Arctostaphylos			
alpina	C	158	
uva-ursi	C	158	
Cassiope			
hypnoides	C	158	
tetragona	C	158	
Erica			
cinerea	C	153	
tetralix	C or B	153	
Kalmia			
latifolia	A	104	Dichogamous
Oxycoccus (*Vaccinium*?)			
gigas	G	154	
Phyllodoca			
coerulea	C	158	
Vaccinium sp.	A	287	Largely self-sterile
myrtillus	C	158	

Family Genus Species	Mode of Reproduction (See Fig. 2)	Reference	Comments
ERICACEAE (cont.)			
Vaccinium (cont.)			
oxycoccus (*Oxycoccus palustris*)	C or B	158	
uliginosum	C	158	
vitis-idaea	C or B	158	
EUPHORBIACEAE			
Alchornea (*Caelebogyne*)			
ilicifolia	G	150	Morphologically dioecious
Aleurites			
fordii	B	10	
montana	A	461	Dichogamous
Euphorbia			
cyparissias	A	104	Self-incompatible
dulces	H	150	
millii (*splendens*)	A	104	Self-incompatible
Hevea			
brasiliensis	A	198, 303	Self-incompatible (some self-compatibility)
Manihot			
esculenta (*utilissima*)	A	208	
Ricinus			
communis	B	99	
EUPOMATIACEAE			
Eupomatia			
laurina	A	162	
FAGACEAE			
Castanea sp.	A	68	
crenata	A	233	Self-incompatible (some self-compatibility)
mollissima	A	283	Self-incompatible
Fagus			
sylvatica	A	311	Self-incompatible (some self-compatibility)
Quercus			
macrocarpa	B or A	386	Probably
robur	A	335	Probably
suber	A	138	Dichogamous
FUMARIACEAE			
Corydalis			
cava	A	104, 385	Self-incompatible
digitata	A	104	Self-incompatible
intermedia	C or B	373	Insufficient evidence
laxa	C or B	373	Insufficient evidence
lutea	A	104	Self-incompatible
pumila	C or B	373	Insufficient evidence
solida	A	373	Self-incompatible
Dicentra			
cucullaria	A	104	Self-incompatible (some self-compatibility)
GENTIANACEAE			
Centaurium			
compressum	B	143	
umbellatum	C	143	

Family Genus Species	Mode of Reproduction (See Fig. 2)	Reference	Comments
GENTIANACEAE (cont.)			
Cotylanthera			
tenuis	H ?	150	
Menyanthes			
trifoliata	A	104	Self-incompatible
GERANIACEAE			
Erodium			
cicutarium var.			
pimpinellifolium	A	104	
macradenum	A	104	
Geranium			
columbinum	C	22	
dissectum	C	22	
molle	C	22	
phaeum	A	22	
pratense	A	22	
purpureum	C	18	
pusillum	C	22	
pyrenaicum	B	22	
robertianum	C	18	2 to 3% natural crossing
rotundifolium	C	22	
sanguineum	C	22	Probably
sylvaticum	A	22	
Pelargonium zonale	A	104	Some self-incompatibility
GESNERIACEAE			
Saintpaulia			
ionantha	–	354	In cultivation pollinated only artificially with manual dehiscence of anthers
GRAMINEAE			
Agropyron			
cristatum	A	396, 65	Self-incompatible
dachystachyum	A	396	Self-incompatible
desertorum	A	396	Self-incompatible
elongatum	A	213	
enysii	B	71	Probably
inerme	A	396	Self-incompatible
intermedium	A	396	Self-incompatible
kirkii	A	71	
parishii	A	405, p. 180	
repens	A	396	Self-incompatible
scabrum (in part)	C	71, 159a	
scabrum (in part)	F	71, 159a	
scabrum (in part)	G	71, 159a	
sibiricum	A	396	Self-incompatible
smithii	A	396	Self-incompatible
spicatum	A	396	Self-incompatible
tenue	B	71	Probably
trachycaulum			
(*pauciflorum*)	C	213	
trichophorum	A	396	Self-incompatible
Agrostis			
alba	A	213, 308	Self-incompatible

Family Genus Species	Mode of Reproduction (See Fig. 2)	Reference	Comments
GRAMINEAE (cont.)			
Agrostis (cont.)			
stolonifera	H	150	
tenuis	D	104, 150	
Alopecurus			
alpinus	G	337	
myosuroides (*agrestis*)	A	104	Self-incompatible
pratensis	A	179, 65	
Amphicarpon			
floridanum	C	457	
purshii	C	104, 457	
Andropogon			
annulatus (*Dicanthium annulatum*)	C	318	
caricosus (*Dicanthium caricosum*)	C	318	
gerardi	A	213	
intermedius (*Bothriochloa intermedia*)	C	318	
scoparius	A	213	
Apera			
spica-venti	A	104	Self-incompatible
Arctagrostis			
latifolia	G	150	
Arrenatherum			
elatius	A	396	Self-incompatible
Avena			
byzantia	C	186	
fatua	C	150	
sativa	C	342, 136, 465	
strigosa	C	150	
Bouteloua			
curtipendula	A	213	
c. "Tuscon" strain	D or G ?	169	
gracilis	A (H ?)	213, 150	
hirsuta	H ?	150	
Briza			
media	A	104	Self-incompatible
Bromus			
carinatus	C	213, 167, 168	
catharticus	C	213	
erectus	A	396	Self-incompatible
inermis	A	396, 65, 469, 1	Self-incompatible (some self-compatibility)
mollis (including *B. hordeaceous*)	C	241	
pumpellianus	A	213	
***secalinus*	A C	104 180	Self-incompatible
Buchlöe			
dactyloides	A	278	Dioecious

Family Genus Species	Mode of Reproduction (See Fig. 2)	Reference	Comments
GRAMINEAE (cont.)			
Calamagrostis			
arundinacea	A	313	
canadensis	H (not G)	315	
canescens	A	313	
chalybaea	G	313	
epigeios	A	313	Some self-incompatibility
inexpansa	H (not G)	315	
langsdorfi	H (not G)	313	
lapponica	G	313	
neglecta	A	313	
purpurascens	H	315	
purpurea	G	313	
varia	A	313	
Cenchrus			
setigerus	G	121, 398	
Coix			
lacryma-jobi	A	448	
Cynodon			
dactylon	A	213, 51	
Cynosurus			
cristatus	A	180	
Dactylis			
glomerata	A	396	Self-incompatible (self-compatibility occurs)
Danthonia			
spicata	C	104	
Deschampsia			
alpina	G	150, 474	
caespitosa	D	150, 474	Depends on locality (see p. 152)
flexuosa	A	104	Self-incompatible
litoralis	A	150	
rhenana	H	150	
Dichelachne			
crinita	C	72	
Digitaria			
exilis	C	75	
Diplachne			
serotina	C	104	
Echinochloa			
crus-galli (*Panicum crus-galli* var. *frumentaceum*)	C	481	
Ehrharta			
calycina	A	371	
Eleusine			
coracana	C	350	Ca. 1% natural crossing
Elymus			
angustus	A	396	Self-incompatible
canadensis	C	213	
chinensis	A	396	Self-incompatible
condensatus	A	396	Self-incompatible
giganteus	A	396	Self-incompatible

Family Genus Species	Mode of Reproduction (See Fig. 2)	Reference	Comments
GRAMINEAE (cont.)			
Elymus (cont.)			
glaucus	C	180	
junceus	A	396	Self-incompatible
triticoides	A	396	Self-incompatible
virginicus	C	213	
Eragrostis			
curvula	C	180	
trichodes	C	213	
Euchlaena			
mexicana (*E.* sp.)	A	355	
Festuca			
arundinacea	A	76, 206	Variable self-incompatibility
ciliata	C	104	
elatior (*pratensis*)	A	104, 270	
myuros	C	104	
novae-zelandiae	A	72a	
ovina	D or G	396, 443	Self-incompatible when sexual; obligate and facultative biotypes found
rubra (in part)	D	104, 150	When sexual, complete range from self-incompatibility to self-compatibility found
sciuroides	C	104	
vivipara	H	150, 474	
Holcus			
lanatus	A	104	Self-incompatible
Hordeum			
brevisubulatum	A	396	Self-incompatible
bulbosum	A	396	Self-incompatible
vulgare	C	342, 408, 423	
Koeleria			
cristata	A	396	Self-incompatible
Leersia			
oryzoides	C	104	
Lolium			
loliaceum	C	205	
multiflorum	A	205	
perenne	A	147	
remotum	C	205	
rigidum	A	205	
temulentum	C	205	
westerwoldicum	A	308	Self-incompatible
Molinia			
caerulea	A	104	Self-incompatible
Oryza			
minuta	A	297	
sativa	C	35, 251, 292	
Oryzopsis			
hymenoides	A	396	Self-incompatible
Panicum			
maximum	H (G ?)	455	

Family Genus Species	Mode of Reproduction (See Fig. 2)	Reference	Comments
GRAMINEAE (cont.)			
Panicum (cont.)			
miliaceum	C	278	
miliare	C	481	
virgatum	D	213	
Paspalum			
dilitatum	H	213, 395	
d. "Common" strain	G		
notatum "Common"	G	52	
n. "Pensacola"	A	53, 54	Self-incompatible
scrobiculatum	C	481	
Pennisetum			
ciliare	G	121, 398	
clandestinum	G	192, 307	Perhaps rarely sexual
glaucum (*typhoides*)	A	278, 228	Self-incompatible (some self-compatibility)
orientale	H	307	Probably a facultative apomict
ramosum	H	307	Probably a facultative apomict
setaceum	H (not G)	307	
villosum	G	307	
Phalaris			
arundinacea	A	396	Self-incompatible
Phleum			
graecum	A	396	Self-incompatible
phleoides	A	396	Self-incompatible
pratense	A	104	Self-incompatible
Phragmites			
communis	G	271	Produces sexual seed very rarely
Poa			
alpigena	G	111	Sexual types probably found also
alpina (in part)	G	111, 150, 314	Sexual types also found—A
ampla	H	314	
arachnifera	A	213	Dioecious
arctica	G	111	Sexual types probably found also
arida	H	314	
bulbosa (in part)	H	150	
chapmaniana	C	456	
compressa	H	150	
glauca	H	150	
irrigata	H	269	
nemoralis	H	150	
nervosa (*nevrosa*)	H	314	One strain is sexual
palustris	H	150	
pratensis	D	13, 3	5 to 10% sexual seed formed Fully sexual types also found
scabrella	H	314	
trivialis	A	150	
Puccinellia			
distans	A	396	Self-incompatible
phryganodes	G	150	

Family Genus Species	Mode of Reproduction (See Fig. 2)	Reference	Comments
GRAMINEAE (cont.)			
Saccharum			
officinarum	A	77	
spontaneum	A	102	Dichogamous
Secale			
cereale	B	182, p. 217, 401	Variable self-incompatibility; 50% natural crossing
turkestanicum	C	41	
Setaria			
italica	C	286	
sphacelata	A	142	
Sieglingia (*Triodia*)			
decumbens	C	104	
Sitanion			
jubatum	C	405, p. 180	
Sorghum			
halapense	A	40	Self-incompatible
vulgare	B	387, 193, 182, p. 368	
sudanense (*vulgare* var. *sudanense*)	B	134	18 to 76% natural crossing
Sporobulus			
airoides	C	180	
cryptandrus	C	180	
Stipa spp.	C or B	213, 168	
viridula	C	180	
Tripsacum			
dactyloides (sp.)	D	355, 117	Ca. 50% sexual seed; an outbreeder
Trisetum			
flavescens	A	308	Self-incompatible
spicatum	H	150	
Triticum			
aestivum (*vulgare*)	C	342, 178, 135	
durum	C	178	
Zea			
mays	A	342, 174, 458	95% natural crossing
Zoysia			
japonica	A or B	123, 124	*Minimum* natural crossing of 65% observed
tenuifolia	A ?	123	Self-incompatible ?
GUTTIFERAE			
Garcinia			
mangostana	G	187	
Rheedia			
brasiliensis	H	187	
macrophylla	H	187	
HAMAMELIDACEAE			
Liquidambar			
styraciflua	A	331a	Self-incompatible (four individuals tested)

Family Genus Species	Mode of Reproduction (See Fig. 2)	Reference	Comments
HYPERICACEAE			
Hypericum			
calycinum	A	104	Self-incompatible
perforatum	G	404	Slight sexuality
ILLECEBRACEAE			
Herniaria			
ciliata	C	67 (cited in 22)	
glabra	C	67 (cited in 22)	
hirsuta	C	67 (cited in 22)	
Illecebrum			
verticillatum	C	67 (cited in 22)	
IRIDACEAE			
Freesia sp.	A	55	Self-incompatible
Iris			
pseudoacorus	A	219	
Marica (*Neomarica*)			
northiana	A	104	Self-incompatible
Romulea			
bubocodium	A	104	Self-incompatible
Thelisia			
planifolia	H	116	
JUGLANDACEAE			
Carya			
illinoensis (*pecan*)	A	148	Some varieties dichogamous
Juglans			
regia	A	148	Dichogamous
JUNCACEAE			
Luzula			
campestris	A	219	Dichogamous
purpurea	C	59	
LABIATAE			
Galeopsis			
bifida	B	150	5 to 10% natural crossing
pubescens	A	150	
speciosa	A	150	
tetrahit	B	150	5 to 10% natural crossing
Lamium			
album	B ?	219	
amplexicaule	C	150	
hybridum	C	150	
intermedium	C	150	
purpureum	C	150	
Mentha			
piperita	C	200	
Origanum			
vulgare	A	261	
Prunella			
vulgaris	A	18	
Rosmarinus			
officinalis	A	309	

Family Genus Species	Mode of Reproduction (See Fig. 2)	Reference	Comments
LAURACEAE			
Persea			
americana	A	415	Dichogamous
caerulea	A	393	Dichogamous
LEGUMINOSAE			
Acacia			
decurrens	A	334	Ca. 90% natural crossing
d. var. *mollis* (*mollissima*)	A	334, 293a	Ca. 86% natural crossing
Albizia (*Albizzia*) sp.	B ?	99a	
Alysicarpus			
buplurifolius	C	399a	
longifolius	A	399a	
pubescens	A	399a	
rugosus var. *heyneanus*	A	399a	
r. var. *styracifolius*	C	399a	
vaginalis	C	399a	
Anthyllis			
vulneraria	A	220, 300	Probably
Apios			
americana (*tuberosa*)	A	104	Possibly self-incompatible
Arachis			
hypogaea	C	353, 182, p. 660	
Astragalus			
sinicus	A	422	
Cajanus			
cajan (*indicus*)	B	226, 470, 291	15% natural crossing
Caragana			
arborescens	A	78	Some self-incompatibility
frutex	A	79	Some self-incompatibility
pygmaea	A	79	Self-incompatible
spinosa	A	79	Self-incompatible
Ceratonia			
siliqua	A	45	Dioecious (hermaphrodites occur)
Cicer			
arietinum	C	349, 444, p. 1014	
Crotalaria sp.	C	213	
***juncea*	C	180	
	A	190, 328	Self-incompatible
spectabilis	C	180	
Cytisus (*Sarothamnus*)			
scoparius	A	219	
Derris			
elliptica	C	441	
malaccensis	C	441	
Dolichos			
lablab	C	350a	
Erythrina			
crista-galli (*speciosa*)	A	104	Self-incompatible
senegalensis	A	104	Self-incompatible

Family Genus Species	Mode of Reproduction (See Fig. 2)	Reference	Comments
LEGUMINOSAE (cont.)			
Gleditsia			
triacanthos	A	481a	Polygamo-dioecious
Glycine			
max	C	182, p. 700	
Hedysarum			
coronarium	A	326	
Indigofera			
arrecta	A	190	
glandulosa	B	97	
sumatrana	A	190	
Kennedya			
beckxiniana	C	357	
carinata	C	357	
coccinea	C	357	
nigricans	C	357	
prorepens	C	357	
prostrata	C	357	
rubicunda	C	357	
stirlingii	C	357	
Lathyrus spp.	C	213	
cicerea	C	326	
grandiflorus	A	104	Self-incompatible
sativus	C	180	
tingitanus	C	180	
Lens			
culinaris (*esculenta*)	C	326	
Lespedeza			
cuneata	B	409, 284	See p. 153
daurica	B	165, 166	
floribunda	B	165, 166	
hedysaroides	B	165, 166	
inschanica	B	165, 166	
latissima	B	165, 166	
repens	B	165, 166	
stipulacea	B	164, 165	
striata	C	213	
stuevei	B	165, 166	
virgata	B	165, 166	
virginica	B	165, 166	
Lotus			
corniculatus	A	104	Self-incompatible
tenuis	A	201	Self-incompatible
uliginossus	A	220, 278	Self-incompatible
Lupinus			
albus	B	366	Ca. 10% natural crossing
angustifolius	C	152, 451	
luteus	B	152, 451, 151	10 to 25% natural crossing
polyphyllus	B	219	
Medicago			
falcata	A	213, 182, p. 733	

Family Genus Species	Mode of Reproduction (See Fig. 2)	Reference	Comments
LEGUMINOSAE (cont.)			
Medicago (cont.)			
hispida	C	213	
lupulina	C	213	
sativa	A	13	
Melilotus			
alba	B	239, 125	
officinalis	A	239, 213	
suaveolens	A	213	
Onobrychis			
viciaefolia var. *sativa*	A	434	Largely self-incompatible
Ornithopus			
sativus	B	240	
Phaseolus			
aconitifolius	C	278	
aureus	C	278	
***coccineus* (*multiflorus*)	B	211	29% natural crossing
	A	27, 244	Some self-incompatibility
lunatus	C to B	274, 273, 25, 6	From 0 to 83% natural crossing
mungo	C	278	
radiatus	C	356	
vulgaris	C (B ?)	272, 25	
Pisum			
sativum	C (B)	171, 182, p. 645, 172b	Most varieties show negligible amounts of natural crossing; a few show more than 25% natural crossing
Styzolobium sp.	C	352	
Swainsona spp.	C	196, 357	
Tephrosia			
virginiana	A	237	
vogelii	A	344	Self-incompatible
Trifolium			
alexandrinum	A	104	Self-incompatible
alpestre	A	104	Self-incompatible
badium	A	104	Self-incompatible
dubium	C	180	
fragiferum	C	213	
glomeratum	C	213	
hybridum	A	278	Self-incompatible (some self-compatibility)
incarnatum	A	104	Self-incompatible
medium	A	104	Self-incompatible
nigrescens	A	48	Self-incompatible
pratense	A	213	Self-incompatible
repens	A	12	Variable self-incompatibility
subterraneum	C	213, 18	
Ulex			
europaeus	A	219	
Vicia			
ervilia	C	326	
faba	B	194, 130, 131	30 to 50% natural crossing

Family Genus Species	Mode of Reproduction (See Fig. 2)	Reference	Comments
LEGUMINOSAE (cont.)			
Vicia (cont.)			
******sativa***	A C	182, p. 654 278, 73	
villosa	A	380, 421	
Vigna			
cylindrica (*catjang*)	C	278	
sinensis	C	278	
Voandzeia			
subterranea	B	75	60 to 80% natural crossing
LEMNACEAE			
Wolffia			
arrhiza	G	150	Rarely flowers, never in temperate zones
LILIACEAE			
Aloe			
aethiopica	A	104	Self-incompatible
barbadensis (*vera*)	A	104	Self-incompatible
cassia	A	104	Self-incompatible
pluridens	A	104	Self-incompatible
Asparagus			
officinalis	A	397	Dioecious (andromonoecy occurs)
Colchicum			
autumnale	A	104	Self-incompatible
Convalleria			
majalis	A	417	Self-incompatible (self-compatibility occurs)
Dianella			
tasmanica (in part)	H	314	
Fritillaria			
camschatcensis	G	150	
imperialis (one race)	G	150	A sexual race also occurs
Gagea			
fistulosa	G	150	
spathaea	G	150	
Gasteria			
brevifolia	A	104	Self-incompatible
lingua	A	104	Largely self-incompatible
nigricans	A	104	Self-incompatible
planifolia	A	104	Self-incompatible
pulchra	A	104	Self-incompatible
sulcata	A	104	Largely self-incompatible
verrucosa	A	104, 385	Self-incompatible
Gloriosa			
superba	A	265	
Haworthia			
attenuata	A	104	Self-incompatible (some self-compatibility)
cymbiformis	A	104	Self-incompatible (some self-compatibility)
tortuosa	A	104	Self-incompatible (some self-compatibility)

Family Genus Species	Mode of Reproduction (See Fig. 2)	Reference	Comments
LILIACEAE (cont.)			
Hemerocallis			
dumortieri	A	104	Self-incompatible
flava	A	104	Self-incompatible
fulva	G	150	
thunbergii (*serotina*)	A	104	Self-incompatible
Hosta			
ventricosa (*caerulea*)	H (not G)	150	
Hyacinthus			
orientalis	A	295	Self-incompatible (as diploid)
Lilium			
aurantum	A	104	Self-incompatible
bulbiferum	D	150	Self-incompatible when sexual
b. var. *croceum* (*croceum*)	A	104	Self-incompatible
canadense	A	104	Self-incompatible
***candidum*	A	104	Self-incompatible (however, described as self-fertile by Cappelletti (56)
chalcedonicum	A	104	Self-incompatible
dauricum	A	104	Self-incompatible
formosanum	A	259	Self-incompatible
hansonii	A	104	Self-incompatible
henryi	A	104	Self-incompatible
humboldtii	A	104	Self-incompatible
japonicum	A	104	Self-incompatible
kelloggii	A	104	Self-incompatible
leichtlinii	A	104	Self-incompatible
longiflorum	A	104	Self-incompatible (some self-compatibility)
maculatum (*elegans*)	A	104	Self-incompatible
martagon	A	104	Self-incompatible
myriophyllum (*sulphureum*)	A	104	Self-incompatible
pardalinum	A	104	Self-incompatible
parryi	A	104	Self-incompatible
parvum	A	104	Self-incompatible
philadelphicum	A	104	Self-incompatible
pumilum (*tenuifolium*)	A	104	Self-incompatible
regale	G	36	
sargentiae	A	104	Self-incompatible
speciosum	A	104	Self-incompatible
superbum	A	104	Self-incompatible
tigrinum	A	104	Self-incompatible
willmottiae (*warleyense*)	A	104	Self-incompatible
Scilla			
nonscripta (*nutans*)	C	219	
Smilacina			
racemosa	G	143a	Probably
Trillium			
erectum	G	203	
grandiflorum	G	203	
sessile	G	203	
undulatum	G	203	

Family Genus Species	Mode of Reproduction (See Fig. 2)	Reference	Comments
LILIACEAE (cont.)			
Tulipa			
armena	A	445	Self-incompatible
celsiana (persica)	A	445	Self-incompatible
chrysantha	A	445	Self-incompatible
clusiana	A	445	
fosteriana	A	445	Self-incompatible
gesneriana	D	150, 445	Self-incompatible when sexual
hageri	A	445	Self-incompatible
kaufmanniana	A	445	
kolpakowskiana	A	445	Self-incompatible
linifolia	A	445	
micheliana	A	445	Self-incompatible
oculis solis	A	445	Self-incompatible
praestans	A	445	
stellata	A	445	
sylvestris	A	445	
turkestanica	A	445	
violacea	A	445	Self-incompatible
Urginea (Scilla)			
maritima	A	344	Self-incompatible
Uvularia			
perfoliata	A	104	Self-incompatible
LINACEAE			
Linum			
austriacum	A	428	Self-incompatible (self-compatibility found)
grandiflorum	A	428	Self-incompatible
monogynum	A	104	Self-incompatible
perenne	A	428	Variable self-incompatibility
usitatissimum	C	98, 225	Ca. 3% natural crossing
LOBELIACEAE			
Lobelia			
fulgens	A	104	Self-incompatible
LORANTHACEAE			
Viscum			
album	B ?	204	
LYTHRACEAE			
Cuphea			
purpurea	A	104	Self-incompatible
Lythrum			
salicaria	A	385	Self-incompatible
MAGNOLIACEAE			
Liriodendron			
tulipifera	B	57	Indirect evidence: vigor of open-pollinated seedlings intermediate to those resulting from selfing or crossing
MALPHIGIACEAE			
Hiptage			
madablota	H	150	
MALVACEAE			
Abutilon			
darwinii	A	104	Self-incompatible
hybridum	A	385	Self-incompatible

Family Genus Species	Mode of Reproduction (See Fig. 2)	Reference	Comments
MALVACEAE (cont.)			
Abutilon (cont.)			
striatum	A	104	Self-incompatible
***theophrasti* (*avicennae*)	C	42	
	A	300	Self-incompatible
venosum	A	104	Self-incompatible
Althaea			
ficifolia	A	104	Self-incompatible
Gossypium			
arboreum	C	2	2% natural crossing in Punjab
barbadense	B	24, 234	5 to 10% natural crossing
hirsutum	B	389, 405a	See p. 152
Hibiscus			
cannabinus	B	427	2 to 45% natural crossing
esculentus	B	345	4 to 19% natural crossing
sabdariffa	C	190, 439, 375	
syriacus	A	104	Self-incompatible
Urena			
lobata	C	350a	
MARANTACEAE			
Maranta			
arundinacea	H ?	300	
MARCGRAVIACEAE			
Marcgravia			
cuyuniensis	C	14	
purpurea	C	14	
MORACEAE			
Cannabinus			
sativa	A	278	Dioecious
Ficus			
carica	A	138	Dioecious
Humulus			
lupulus	A	278	Dioecious
Morus			
alba	A	137	Dioecious
MUSACEAE			
Musa spp.	A	198	Variable types of sterility found
Strelitzia			
reginae	A	55	
MYRISTICACEAE			
Myristica			
fragrans	A	63	Dioecious
MYRTACEAE			
Eucalyptus			
alba	A	246	Self-incompatible
grandis	A	246	Self-incompatible
maculata	A	246	Self-incompatible
m. var. *citriodora* (*citriodora*)	A	246	Self-incompatible
punctata	A	246	Self-incompatible
robusta	A	246	Self-incompatible
umbellata	A	246	Self-incompatible

Family Genus Species	Mode of Reproduction (See Fig. 2)	Reference	Comments
MYRTACEAE (cont.)			
Eugenia			
javanica	A	336	Self-incompatible
paniculata (*hookeri*)	H	150	
Feijoa			
sellowiana	A	384	Self-incompatible (self-compatibility occurs)
Psidium			
guajava	A or B ?	372	Self-fertile, ". . . natural crossing is very common"
Syzygium (*Eugenia*)			
aqueum (*aquea*)	G	336	Produces no pollen
cuminii (*cumini*)	A	336	Self-incompatible (perhaps apomictic—150)
jambos	G	336	
malaccense (*malaccensis*)	H	336	
NYCTAGINACEAE			
Bougainvillea			
spectabilis	A	104	Self-incompatible
OCHNACEAE			
Ochna			
serrulata	G	150, 404	
OLEACEAE			
Forsythia			
intermedia	A	293	Self-incompatible
Fraxinus			
americana	A	473a	Dioecious
excelsior	A	473a	Polygamodioecious
pennsylvanica	A	473a	Dioecious
velutina	A	473a	Dioecious
Olea			
europaea	A or B	148, 46, 47	Some varieties are self-incompatible
Syringa			
vulgaris	A	479	
ONAGRACEAE			
Anogra (*Oenothera*)			
pallida	G	210	
Circaea			
intermedia	G	150	
Clarkia	B	262	Data on individual spp. not given
biloba	B	368	
cylindrica	A	262	
epilobioides	C	262	
lingulata	A	262a	
Isnardia			
palustris	C	238	
Jussiaea (*Jussieua*)			
grandiflora	A	104	Self-incompatible
Oenothera			
acaulis	A	104	Self-incompatible

Family Genus Species	Mode of Reproduction (See Fig. 2)	Reference	Comments
ONAGRACEAE (cont.)			
Oenothera (cont.)			
caespitosa			
var. *marginata*	A	104	Self-incompatible
c. var. *montana*	A	104	Self-incompatible
californica	A	104	Self-incompatible
macrosiphon	A	104	Self-incompatible
organensis	A	258	Self-incompatible
speciosum	A	259	Self-incompatible
Taraxia			
ovata	H ?	150	
ORCHIDACEAE			
Anacamptis			
pyramidalis	A	156	
Blztilla			
striata	H	150	Facultative, yielding haploids
Cephalanthera			
rubra	F	150, 156a	Autogamous, but in nature propagates principally asexually
Chamaeorchis			
alpina	C	157	
Coeloglossum			
viride	B ?	156	
Cypripedium			
calceolus	A	104	Self-incompatible
Epidendrum			
cinnabarium	A	104	Self-incompatible
Epipactis			
atropurpurea	B ?	156	
atrorubens	A	104	Self-incompatible
confusa	C	480	
helleborine	C	156, 462, 183a	
latifolia	E	276, 150	Facultatively apomictic, yielding haploids
leptochila	C	480	
palustris	C	156	
persica	C	156	
phyllanthes	C	480	
purpurea	C	156	
Epipogium			
aphyllum	D	156, 150	Seed-formation rare, spreading by runners
Goodyera			
repens	B ?	156	
Habenaria			
hyperborea	C	156	
Herminium			
monorchis	B	156	
Leucorchis			
albida	C ?	156	
Maxillaria			
atrorubens	A	104	Self-incompatible

Family Genus Species	Mode of Reproduction (See Fig. 2)	Reference	Comments
ORCHIDACEAE (cont.)			
Nigritella			
nigra (in part)	G	150	Scandinavian forms with high chromosome numbers (Central European forms with low chromosome numbers are sexual)
Oncidium			
cavendishianum	A	104	Self-incompatible
cimiferum	A	104	Self-incompatible
crispum	A	104	Self-incompatible
divaricatum	A	104	Self-incompatible
lemonianum	A	104	Self-incompatible
microchilum	A	104	Self-incompatible
sphacelatum	A	104	Self-incompatible
unicorne	A	104	Self-incompatible
Ophrys			
apifera	C	276	
Orchis			
latifolia	B	276	
maculata	E	276, 150	Facultatively apomictic, yielding haploids
morio	B	276	
Phaius (*Phajus*)			
bernaysii	C	369	
grandifolius	C	369	
wallichii	C	156	
Spathoglottis			
plicata	C	156	
Spiranthes			
australis	H	156	
cernua (in part)	G	254	Sexual forms known
spiralis	B	156	
Vanilla			
coursii	B	438	Probably
humblotii (sic)	B	438	Probably
madagascariensis	B	438	Probably
planifolia (*fragrans*)	C	438	In commercial plantings in Madagascar, where hand-pollinated
Zeuxine			
sulcata	G	424	
Zygopetalum			
mackayi	H ?	150	
OROBANCHACEAE			
Cistanche			
lutea	C	104	
OXALIDACEAE			
Oxalis			
valdiviensis (*valdiviana*)	A	132, 104	Self-incompatible
PALMACEAE			
Archontophoenix			
cunninghamiana (*cunninghamii*)	A	392	

Family Genus Species	Mode of Reproduction (See Fig. 2)	Reference	Comments
PALMACEAE (cont.)			
Cocos			
nucifera	A, B, or C	198, 267 482	Varies with variety, e.g., Tall palm: A, King palm and Dwarf palm: C.
Elaeis			
guineensis	A	198, 118	
Phoenix			
dactylifera	A	179	Dioecious
PAPAVERACEAE			
Chelidonium			
majus	A	109	
Eschscholzia			
californica	A	104	Self-incompatible
Hypecoum			
grandiflorum	A	104	Self-incompatible
procumbens	A	104	Self-incompatible
Papaver			
alpinum	A	104	Self-incompatible
nudicaule (*radicatum*)	A	104	Self-incompatible
rhoeas	A	104	Self-incompatible
somniferum	A	198	
PASSIFLORACEAE			
Passiflora			
alata	A	104	Self-incompatible
caerulea	A	104	Self-incompatible
edulis	A	104	Self-incompatible
gracilis	A	104	
laurifolia	A	104	Self-incompatible
quadrangularis	A	104	Self-incompatible
racemosa	A	104	Self-incompatible
vitafolia	A	104	Self-incompatible
PEDALIACEAE			
Sesamum			
indicum (*orientale*)	B	249, 388 248	Ca. 5% natural crossing
PINACEAE			
Larix			
gmelinii (*dahurica*)	B	335	Probably
decidua (*europaea*)	B	335	Probably
laricina	A	335	Self-incompatible
leptolepis	B	335	Probably
sibirica	B	335	Probably
Picea			
abies	B	250	
Pinus sp.	A	464, 214	
echinata	A	481a	Probably
caribaea (*elliottii*)	A	481a, 291a	Probably
monticola	A	43a	
nigra (*n.* var. *austriaca*)	A	212	
taeda	A	481a	
Pseudotsuga			
taxifolia	A	7, 322	Self-incompatible (some self-compatibility)

Family Genus Species	Mode of Reproduction (See Fig. 2)	Reference	Comments
PIPERACEAE			
Piper			
nigrum	A (H ?)	139	Variably dioecious; possibly apomictic in part
PLANTAGINACEAE			
Plantago			
juncoides	A	146	Dichogamous
lanceolata	A	18	
major	A	18	
maritima	A	146	Self-incompatible
ovata	A	61	Since 65% male sterile
rhodosperma	C	61	
virginica	C	104	
wrightiana	C	61	
PLATANACEAE			
Platanus sp.	A	138	Dichogamous
PLUMBAGINACEAE			
Acantholimon			
acerosum	A	22	Self-incompatible
armenum	A	22	Self-incompatible
caespitosum	A	22	Self-incompatible
creticum	A	22	Self-incompatible
echinus	A	22	Self-incompatible
glumaceum	A	22	Self-incompatible
olivieri	A	22	Self-incompatible
Armeria			
canescens	A	22	Self-incompatible
gaditana	A	22	Self-incompatible
juniperifolia	A	22	Self-incompatible
maritima ssp. *alpina*	A	22	Self-incompatible
m. ssp. *californica*	B	18	
m. ssp. *elongata*	A	22	Self-incompatible
m. ssp. *halleri*	A	22	Self-incompatible
m. ssp. *maritima*	A	18, 22	Self-incompatible (some self-compatibility)
m. ssp. *sibirica*	C	18	
mauritanica	A	22	Self-incompatible
plantaginea	A	22	Self-incompatible
welwitschii	A	22	Self-incompatible
Ceratostigma spp.	A	22	Heterostylous
Goniolimon			
callicomum	A	19	Self-incompatible
eximium	A	19	Self-incompatible
kaufmannianum	A	19	Self-incompatible
speciosum	A	19	Self-incompatible
Limoniastrum			
guyonianum	A	22	Self-incompatible
monopetalum	A	22	Self-incompatible
Limonium			
alberti	A	19	Self-incompatible
arabicum	A	19	Self-incompatible
arborescens	A	19	Self-incompatible
articulatum	A	19	Self-incompatible
asparagoides	A	19	Self-incompatible
aureum	A	19	Self-incompatible

Family Genus Species	Mode of Reproduction (See Fig. 2)	Reference	Comments
PLUMBAGINACEAE (cont.)			
Limonium (cont.)			
axillare	A	19	Self-incompatible
bahamense	A	19, 20	Self-incompatible
bellidifolium	A	19, 17	Self-incompatible
bicolor	A	19	Self-incompatible
binervosum (including: *L. paradoxum*, *L. recurvum*, *L. transwallianum*)	H	18	
bonduellii	A	19	Self-incompatible
bourgaeii	A	19	Self-incompatible
brasiliense	A	19	Self-incompatible
brassicifolium	A	19	Self-incompatible
braunii	A	19	Self-incompatible
brunneri	A	19	Self-incompatible
cabulicum	A	19	Self-incompatible
caesium	A	19	Self-incompatible
campanyonis	H	22	
chrysocomum	A	19	Self-incompatible
confusum (*Statice oleaefolia* var. *confusa*)	G	8, 22	
corculum	A	19	Self-incompatible
cordatum	A	19	Self-incompatible
cosyrense	H	19	
cumanum	A	19	Self-incompatible
cylindrifolium	A	19	Self-incompatible
decipiens	A	19	Self-incompatible
delicatulum	H	22	
densiflorum (in part)	A	22	Self-incompatible
" (in part)	H	22	
dichotomum	A	19	Self-incompatible
dictyocladum	A	19	Self-incompatible
diffusum	A	19	Self-incompatible
dodartii	H	22	
dregeanum	A	19	Self-incompatible
dubyi	A	19	Self-incompatible
dufourii	H	22	
durieni	A	22	Self-incompatible
duriusculum	A	22	Self-incompatible
echioides	H	22	
effusum	A	19	Self-incompatible
equisetinum	A	19	Self-incompatible
ferulaceum	A	19	Self-incompatible
flexuosum	A	19	Self-incompatible
gilesii	A	19	Self-incompatible
girardianum	H	22	
globuliferum	A	19	Self-incompatible
gmelinii	A	19	Self-incompatible
gougetianum	H	22	
graecum	A	22	Self-incompatible
griffithii	A	19	Self-incompatible
guaicuru (*chilense*)	A	19	Self-incompatible

Family Genus Species	Mode of Reproduction (See Fig. 2)	Reference	Comments
PLUMBAGINACEAE (cont.)			
Limonium (cont.)			
humboldtii	A	19	Self-incompatible
imbricatum	A	19	Self-incompatible
jovibarbum	A	19	Self-incompatible
kraussianum	A	19	Self-incompatible
latifolium	A	19	Self-incompatible
leptostachyum	A	19	Self-incompatible
linifolium	A	19	Self-incompatible
lychnidifolium	H	18	
macrophyllum	A	19	Self-incompatible
macropterum	A	19	Self-incompatible
macrorhabdon	A	19	Self-incompatible
mauritanicum	A	19	Self-incompatible
meyeri	A	19	Self-incompatible
minutum	A	19	Self-incompatible
mucronatum	A	19	Self-incompatible
multiflorum	A	22	Self-incompatible
nudum	A	19	Self-incompatible
ocymifolium	H	22	
ornatum	A	19	Self-incompatible
ovalifolium	A	22	Self-incompatible
owerinii	A	19	Self-incompatible
papillatum	A	19	Self-incompatible
patagonicum	A	19	Self-incompatible
pectinatum	A	19	Self-incompatible
perezii	A	19	Self-incompatible
perfoliatum	A	19	Self-incompatible
preauxii	A	19	Self-incompatible
pruinosum	A	19	Self-incompatible
psilocladon	A	22	Self-incompatible
puberulum	A	19	Self-incompatible
reflexum	H	22	
salsuginosum	H	22	
scabrum	A	19	Self-incompatible
schrenkianum	A	19	Self-incompatible
sieberi	A	22	Self-incompatible
sinense	A	19	Self-incompatible
sinuatum	A	19	Self-incompatible
somalorum	A	19	Self-incompatible
spathulatum	A	22	Self-incompatible
spicatum	A	19	Self-incompatible
stocksii	A	19	Self-incompatible
suffruticosum	A	19	Self-incompatible
suworowii	A	19	Self-incompatible
tataricum (*Goniolimon tataricum*)	A	19	Self-incompatible
tenellum	A	19	Self-incompatible
thouinii	A	19	Self-incompatible
tomentellum	A	19	Self-incompatible
tuberculatum	A	19	Self-incompatible
tubiflorum	A	19	Self-incompatible
uruguayense	A	19	Self-incompatible
virgatum	A	19	Self-incompatible

Family Genus Species	Mode of Reproduction (See Fig. 2)	Reference	Comments
PLUMBAGINACEAE (cont.)			
Limonium (cont.)			
vulgare	A	19, 104	Self-incompatible
wrightii	A	19	Self-incompatible
xantholeucum	A	19	Self-incompatible
xipholepis	A	19	Self-incompatible
Plumbago			
capensis	A	22	Self-incompatible
europaea	A	22	Self-incompatible
indica (*rosea*)	A	22	Self-incompatible
Statice			
inarimensis	H	22	
remotispicula	A	22	Self-incompatible
Vogelia spp.	A	22	Self-incompatible
POLEMONIACEAE			
Cobaea			
penduliflora	A	104	Self-incompatible
Collomia			
grandiflora	C	104	
Gilia			
achilleaefolia (in part)	B	144	
" (in part)	C	144	
angelensis	B	144	
capitata	A	144	Self-incompatible (self-compatible races also)
clivorum	C ?	144	
laciniata	C ?	144	
millifoliata	C ?	144	
nevinii	C ?	144	
tricolor	B	144	
Phlox			
drummondii	A	329	At least 80% natural crossing; some self-incompatibility
POLYGONACEAE			
Acetosa			
arifolia	H (not G)	268	
pratensis	H (not G)	268	
thyrsiflora	H (not G)	268	
Atraphaxis			
frutescens	H	150	
Fagopyrum			
esculentum	A	382, 431	Self-incompatible (some self-compatibility)
Koenigia (*Polygonum* ?)			
islandica	C	104	
Oxyria			
digyna (in part)	H	404	
Polygonum			
perfoliatum	C	104	
viviparum	G	404, 150	Sexuality found rarely
Rheum			
palmatum	A	370	Self-incompatible (some self-compatibility)
rhaponticum	A	182, p. 535	

Family Genus Species	Mode of Reproduction (See Fig. 2)	Reference	Comments
POLYGONACEAE (cont.)			
Rumex			
acetosa	H	104, 321, 475	
arifolius	H	104	
nivalis	H	104	
PONTEDERIACEAE			
Pontederia			
cordata	A	181	
PORTULACACEAE			
Montia spp.	C	298	All British species
Portulaca			
grandiflora	A	435a	One strain self-incompatible
PRIMULACEAE			
Anagallis			
arvensis	C	150	
Cortusa			
matthioli	A	104	Self-incompatible
Cyclamen			
persicum	A	104	Self-incompatible
Hottonia			
inflata	C	104	
Lysimachia			
nummularia	G	87	Generally seed-sterile, but self-incompatible when sexual
Primula			
auricula	A	112	Self-incompatible
beesiana	A	112	Self-incompatible
chungensis (in part)	A	112	Self-incompatible
farinosa	A	112	Self-incompatible
floribunda	A	112	Self-incompatible (some self-compatibility)
hirsuta	A	112	Self-incompatible
integrifolia	A	112	Self-incompatible
obconica	A	289	Self-incompatible
poissonii ssp. *wilsoni*	A	112	Self-incompatible
pulverulenta	A	112	Self-incompatible
sinensis	A	280	Self-incompatible
verticillata	B ?	112	
viscosa	A	112	Self-incompatible (some self-compatibility)
vulgaris	A and C	83	Self-incompatible (A) and self-compatible, autogamous (C) types found; selection favors C
Trientalis			
europaea	A	104	Self-incompatible
PROTEACEAE			
Grevillea			
banksii	B	49	
robusta	A	49	
Macadamia			
ternifolia	B	446	Partial self-incompatibility

Family Genus Species	Mode of Reproduction (See Fig. 2)	Reference	Comments
PYROLACEAE			
Monotropa			
hypopitys	C	158	
Pyrola			
minor	C or B	158	
media	C	158	
RANUNCULACEAE			
Aconitum			
napellus	A	219	Dichogamous
Anemone			
nemorosa	B	219	
Aquilegia			
vulgaris	B	9	16% natural crossing
Caltha			
palustris	A	219, 22	Self-incompatible
radicans	A	22	Self-incompatible
Clematis			
vitalba	B	219	
Delphinium			
consolida	A	104	Self-incompatible
elatum	A	104	Self-incompatible
Helleborus			
foetidus	A	104	Self-incompatible
Ranunculus			
acris	A (D)	17, 150	Self-incompatible (ca. 1% apomictic seed formed)
auricomus	G	150	
bulbosus	A	104	Self-incompatible
cassubicifolius	H	150	Probably
cassubicus	G	150	
fallax	G	150	
ficaria (tetraploids)	G	150, 275	
" (diploids)	A		Self-incompatible
hyperboreus	H ?	150	
verna	A	104	Self-incompatible
Trollius			
europaeus	B	219	
RESEDACEAE			
Reseda			
lutea	A	104	Self-incompatible (largely)
odorata	A	104, 107	Self-incompatible (largely)
ROSACEAE			
Agrimonia			
eupatoria	H	150	
Alchemilla			
acutiloba	G	374	
alpina	G	150	
arvensis	G	150	
cymatophylla	G	374	
filicaulis	G	374	
glabra	G	374	
glaucescens	G	374	
glomerulans	G	374	
heptagona	G	374	
hirsuticaulis	G	374	

Family Genus Species	Mode of Reproduction (See Fig. 2)	Reference	Comments
ROSACEAE (cont.)			
Alchemilla (cont.)			
micans	G	374	
murbeckiana	G	374	
nebulosa	G	374	
obtusa	G	374	
pastoralis	G	374	
pentaphyllea	A	150	
plicata	G	374	
propinqua	G	374	
sarmatica	G	374	
subcrenata	G	374	
subglobosa	G	374	
vestita	G	374	
vulgaris	G	150	
wichurae	G	374	
xanthochlora	G	374	
Chaenomeles			
lageneria	A	444, p. 553	Self-incompatible (some self-compatibility)
Cotoneaster spp.	H	377	Numerous apomicts, especially among triploid species (incomplete evidence)
Crataegus spp.	H	150	Numerous apomicts
Cydonia			
oblonga	A	379	Self-incompatible (some varieties self-compatible but still A)
Eriobotrya			
japonica	A	16	Self-incompatible (in two varieties studied)
Fragaria			
chiloensis var. *ananassa*	A or C	91	Pistillate plants A; hermaphrodite plants C
viridis	A	403	Self-incompatible
Geum			
rivale	A	219	Dichogamous
Kerria			
japonica	A	104	Self-incompatible
Malus			
floribunda	A	378	Self-incompatible (probably)
hupehensis	G	94	
platycarpa	A	378	Self-incompatible (probably)
prunifolia	A	378	Self-incompatible (probably)
robusta	A	378	Self-incompatible (probably)
sargentii	H	377	
seiboldii	H (not G)	319	
sylvestris	A or B	148	Some varieties self-incompatible; others not
Neviusia			
alabamensis	A	104	Self-incompatible
Potentilla spp. (in part)	H	150, 314	Numerous apomicts found in this complex genus—see references
bifurca	A	104	Self-incompatible

Family Genus Species	Mode of Reproduction (See Fig. 2)	Reference	Comments
ROSACEAE (cont.)			
Prunus			
amygdalus (*communis*)	A	148	Self-incompatible
armeniaca	A	101	Some varieties self-incompatible
avium	A	148, 80	Self-incompatible
besseyi	A	478	Self-incompatible
cerasus	A or B	148, 80	Variable self-incompatibility
domestica	A or B	148, 80	Varies (some varieties self-incompatible)
lusitanica	A	104	Self-incompatible
pennsylvanica	A	478	Self-incompatible
prostrata	A	104	Self-incompatible
salicina	A	148	Self-incompatible
spinosa	A	219	Dichogamous
tomentosa	A	394	Self-incompatible
Pyrus			
amygdaliformis	A	378	Self-incompatible (probably)
communis	A or B	148, 80	Varies (some varieties self-incompatible)
eleagrifolia	A	378	Self-incompatible (probably)
phaeocarpa	A	378	Self-incompatible (probably)
Rosa			
beggeriana	A	104	Self-incompatible
canina	A	219	Self-incompatible
rugosa	A	104	Self-incompatible
setigera	A	104	Self-incompatible
Rubus spp.	A, H	96, 150, 149, 108	Apomixis common in genus; self-incompatibility found in some of the sexual forms, not all
sp. (*R. rusticanus* var. *inermis* × *R. thrysiger*)	B	176	17% natural crossing
allegheniensis	A	150	Self-incompatible
glaucus	H	90	
idaeus	A	150, 176	95 to 100% natural crossing; self-incompatible ?
odoratus	A	104	Self-incompatible
parvifolius	A	468	Self-incompatible
spectabilis	A	104	Self-incompatible
tomentosus	A	150	
trivialis	A	96	Self-incompatible
ulmifolius	A	150	Self-incompatible
Sorbus			
aria (in part)	H	150	
arranensis	G	264	
chamaemespilus (triploid forms)	G	264	
hybrida	G	264	
intermedia	G	264	
lancifolia	G	264	
meinichii	G	264	
minima	H	150	
mougeoti	G	264	
neglecta	G	264	

Family Genus Species	Mode of Reproduction (See Fig. 2)	Reference	Comments
ROSACEAE (cont.)			
Sorbus (cont.)			
obtusifolia	H	264	
salicifolia	G	264	
subpinnata	G	264	
subsimilis	G	264	
sudetica	H	150	
teodori	G	264	
RUBIACEAE			
Cinchona			
calisaya	A	60	Self-incompatible
ledgeriana	A	60, 110	Self-incompatible
succirubra	A	60	Self-incompatible
Coffea spp. (except *C. arabica*)	A	245	Self-incompatible
arabica	B	245, 430	40 to 90% natural crossing
Gardenia			
thunbergia	A	104	Self-incompatible
Houstonia			
caerulea	A	104	Self-incompatible
Mitchella			
repens	A	104	Self-incompatible
Mussaenda			
luteola	A	104	Self-incompatible
Rudgea			
jasminoides	A	23	Self-incompatible
RUTACEAE			
Citrus spp.	B, E	198, 150, 459	
aurantifolia	H (not G)	459 (Table 44)	
aurantium	H (not G)	459 (Table 44)	
grandis	A or B	459, p. 796	Sexual (probably A or B)
hybrida	H (not G)	459 (Table 44)	
limon	H (not G)	459 (Table 44)	
paradisii	H (not G)	459 (Table 44)	
reticulata	H (not G)	459 (Table 44)	
sinensis	H (not G)	459 (Table 44)	
Ptelea			
trifoliata	H ?	150	
Triphasia			
trifolia (*aurantiola*)	H	150	
Zanthoxylum (*Xanthoxylum*)			
alatum	H ?	314	
bungei	H	314	
SALICACEAE			
Populus spp.	A	189	Dioecious
SAPINDACEAE			
Litchi			
chinensis	B	302, 301	
Nephelium			
lappaceum	A	358	
SAPOTACEAE			
Argania			
sideroxylon	B	331	

Family Genus Species	Mode of Reproduction (See Fig. 2)	Reference	Comments
SAURURACEAE			
Houttuynia			
cordata	G	150	Probably
SAXIFRAGACEAE			
Parnassia			
palustris	B	277	
Philadelphus			
acuminatus	A	339	Self-incompatible
coronarius var. *aureus*	A	339	Self-incompatible
falkoneri	A	339	Self-incompatible
lewisii	A	339	Self-incompatible
microphyllus	A	339	Self-incompatible
nepalensis	A	339	Self-incompatible
pubescens (*latifolius*)	A	339	Self-incompatible
schrenkii	A	339	Self-incompatible
verrucosus	A	339	Self-incompatible
viksnei	A	339	Self-incompatible
Ribes sp.	A	106	
glutinosum	A	317	Self-incompatible
nevadense	A	317	Self-incompatible
roezlii	A	317	Self-incompatible
viscosissimum	A	317	Self-incompatible
Saxifraga			
cernua	G	150	
flagellaris	H ?	150	
stellaris var. *comosa*	G	404, 150	Other varieties sexual, protandrous (A)
Tolmiea			
menziesii	A	104, 385	Self-incompatible
SCROPHULARIACEAE			
Antirrhinum			
barrelieri	A	104	Self-incompatible
glutinosum	A	104, 172a	Self-incompatible
hispanicum	A	104	Self-incompatible
latifolium	A	104	Self-incompatible
linkianum	A	172a	Self-incompatible
meonanthum	A	104, 172a	Self-incompatible
molle	A	104, 172a	Self-incompatible
orontium	C	172a	
ramosissimum	A	172a	Self-incompatible
Digitalis			
lanata	C	109	
purpurea	A	109, 219	
Linaria			
reticulata	A	385	Self-incompatible
Mimulus			
nasutus	C	17	
Nemesia			
capensis	A	364	Self-incompatible
cheiranthus	A	364	Self-incompatible
pageae	A	364	Self-incompatible
platysepala	A	364	Self-incompatible
strumosa	A	364	Self-incompatible
Paulownia			
fortunei	A	104	Self-incompatible

Family Genus Species	Mode of Reproduction (See Fig. 2)	Reference	Comments
SCROPHULARIACEAE (cont.)			
Russelia			
equisetiformis	A	104	Self-incompatible
Scrophularia			
nodosa	A	219	Dichogamous
scapolii	A	104	Self-incompatible
Verbascum			
nigrum	A	104	Self-incompatible
phlomoides	A	104	Self-incompatible
phoeniceum	A	104, 385	Self-incompatible
Veronica			
agrestis	C	150	
chamaedrys	A	219	Dichogamous
filiformis	A	17	Self-incompatible
officinalis	A	18	Self-incompatible
opaca	C	150	
polita	C	150	
syriaca	A	104	Self-incompatible
tournefortii	C	150	
SOLANACEAE			
Atropa			
belladonna	A	109	Dichogamous
Capsicum			
frutescens	B	316	7 to 36% natural crossing
Hyoscyamus			
albus	C	292a	
niger	C	292a	
Lycium			
ovatum	A	104	Self-incompatible
Lycopersicon			
chilense	A	363	Self-incompatible
esculentum	C	256, 230, 216, 361, 362	Ca. 2% natural crossing
glandulosum	A	282	Self-incompatible
hirsutum (except *L. h.* f. *glabratum*)	A	282	Self-incompatible
h. f. *glabratum*	C	376	
peruvianum	A	282	Self-incompatible
Nicotiana			
alata	A	104	Self-incompatible
bonariensis	A	104	Self-incompatible
cavanillesia	A	104	Self-incompatible
pompasana	A	104	Self-incompatible
rustica	C	103	
sanderae	A	104, 385	Self-incompatible
tabacum	C or B	182, p. 1037, 103	2 to 3% natural crossing
Petunia			
axillaris	A	418	Self-incompatible (as diploid) (self-compatible as tetraploid)
hybrida	A	420	Self-incompatible
violacea	A	279, 385	Self-incompatible

Family Genus Species	Mode of Reproduction (See Fig. 2)	Reference	Comments
SOLANACEAE (cont.)			
Solanum			
anomalocalyx	A	347	Self-incompatible
aracc-papa	A	325	Self-incompatible
berthaultii	A	347	Self-incompatible
caldasii	A	346	Self-incompatible
***chacoense*	A	325	Self-incompatible
	C	351	
jamesii	A	325	Self-incompatible
lapazense	A	347	Self-incompatible
melongena	B	229	7% natural crossing
rybinii	A	347	Self-incompatible
simplicifolium	A	347	Self-incompatible
stenotomum	A	347	Self-incompatible
subtilius	A	346	Self-incompatible
tuberosum	C (B)	182, p. 993, 126, 444, p. 411	
yarbari	A	347	Self-incompatible
STERCULIACEAE			
Herrania			
albiflora	A	285	Self-incompatible
balaoense	A	285	Self-incompatible
mariae	A	285	Self-incompatible
Theobroma			
cacao	A or B	172, 323, 343	Some self-incompatibility; when self-compatible, 20 to 40% natural crossing
THEACEAE			
Thea			
sinensis	A	198	Self-incompatible
THYMELAEACEAE			
Edgeworthia			
papyrifera	A ?	306	Self-incompatible
Wikstroemia			
indica var. *viridiflora*	H	150	
TILIACEAE			
Corchorus			
capsularis	C	140, 198	
olitorius	C (B)	190, 140	
TYPHACEAE			
Typha			
angustifolia	A	104	Dichogamous
latifolia	A	104	Dichogamous
ULMACEAE			
Ulmus spp.	A	215	Dichogamous
hollandica belgica	G	255	Seed sterile—pollination does not occur, though pollen is formed
UMBELLIFERAE			
Angelica			
archangelica (*Archangelica officinalis*)	A	109, 93	
Anthriscus			
sylvestris	A	219	Dichogamous

Family Genus Species	Mode of Reproduction (See Fig. 2)	Reference	Comments
UMBELLIFERAE (cont.)			
Apium			
graveolens	C	84, 106	
Daucus			
carota	A	106, 444, p. 306	
Pastinaca			
sativa	B	209, 172b	
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contrayerva	H	150	Probably
drakeana	H	150	Probably
psilurus	H	150	Probably
Elatostema			
acuminatum	G	150	
eurhyncum	G	150	
gracilipes	H	150	Probably
lacinatum	H	150	Probably
latifolium	H	150	
machaerophyllum	H	150	
peltifolium	H	150	
penninerve	H	150	
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